Epiphytic bryophytes and habitat microclimate variation in lower montane rainforest, Peru.

by

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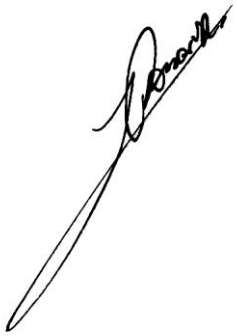
Declaration

This thesis contains no material which has been accepted for the award of any other degree or diploma in any tertiary institution, and to the best of my knowledge and belief, contains no material previously published or written by another person, except where due reference is made in the text of the thesis.

Signed



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Abstract

A survey of epiphytic bryophytes and a study of microclimatic variation within a tree crown were conducted in lower montane rainforest at 2400 m in the Peruvian Yungas. A total of 129 species (87 hepatics, 1 hornwort and 41 mosses) were collected on 3 trees, using different methodologies. A single *Weinmannia* sp. host supported 110 species (77 hepatics, 1 hornwort and 32 mosses). Species with a wide distribution on the hosts made up 47% of the epiphytic assemblage, 22% were limited to the trunks and 31% occurred only in the crowns. The overall hepatic to moss ratio was 2.15:1. Mosses exhibited a narrower distributional range than hepatics. The greatest species richness and abundance was found on the large branches in the mid-crown. Species found in the mid-crown generally had a broader distribution on hosts than those found on the lower trunk or the outer crown. Classification and ordination analyses of the species and environmental data indicated the presence of 4 communities: an outer crown, a mid to mid-outer crown, an upper trunk and a lower trunk community. Species distribution on hosts in the present study appeared to be influenced by the intensity of radiation, particularly diffuse radiation, and relative humidity related to a moisture availability gradient. Temperature appeared least important. Six species were selected as potential microclimate change indicators.

Variation in temperature, relative humidity, visible sky fraction, leaf area index and radiation intensity were measured throughout a single canopy a co-dominant *Weinmannia* sp. The opposing gradients of temperature and relative humidity displayed similar fluctuation patterns as found in lowland rainforest, although the range of the gradients was smaller, possibly due to greater atmospheric mixing facilitated by the more permeable canopy at the montane rainforest study site. Microclimate stability decreased with distance above the ground. The lower trunk micro-habitat was the most humid, coolest and least illuminated. The highest temperature and lowest relative humidity were recorded in the mid-outer crown, closely followed by the most irradiated crown periphery. The above canopy temperature remained cooler during the day than the tree crown. The lowest mean hourly temperature was recorded in the mid-crown, induced by rapid

radiative cooling in the evening. The air above the canopy was warmer at night than any micro-habitat on the tree host.

The study found 27 bryophytes species (5 mosses, 22 hepatics) not previously recorded for Peru. Recommendations for methodology in future bryophyte surveys in Peruvian lower montane rainforest are presented. Future studies must parallel more concerted efforts to raise the awareness of the local population about the ecological importance of bryophytes, particularly in cloud forests.

Resumen

Un estudio de briofitas epifitas y de la variación microclimática dentro de la copa de un árbol fueron conducidos en los bosques mas bajos de montaña a 2400 m. en las Yungas peruanas. Un total de 129 especies (87 hepáticas, 1 antocerota y 41 musgos) fueron recolectadas en 3 árboles, usando diferentes metodologías. En un solo *Weinmannia* sp. se encontró 110 especies (77 hepáticas, 1 antocerota y 32 musgos). Especies con una amplia distribución en los árboles contribuyeron 47% de epifitas, 22% fueron limitados a los troncos y 31% ocurrieron solo en las copas. La totalidad de tasa de hepáticas a musgos fue 2.15:1. Los musgos mostraron un rango de distribución mas estrecho que las hepáticas. La más grande riqueza y abundancia de especies fue encontrada en las ramas grandes de la media copa. Las especies encontradas en la media copa generalmente tuvieron una distribución mas ancha en los árboles que aquellos encontrados en el tronco bajo o en la copa exterior. Los análisis de clasificación y ordenación de las especies y data de medio ambiente indicaron la presencia de 4 comunidades: Copa exterior, de media copa a media copa exterior, parte superior del tronco y la comunidad de la parte baja del tronco. La distribución en los árboles del presente estudio pareció ser influenciada por la intensidad de radiación, particularmente radiación difusa y relativa humedad relacionada a la escala de disponibilidad de agua. La temperatura pareció menos importante. Seis especies fueron seleccionadas como indicadores potenciales del cambio de microclima.

La variación de la temperatura, humedad relativa, fracción visible de cielo, índice de la área foliar e intensidad de radiación fueron medidos en todas partes de un co-dominante *Weinmannia* sp. Las escalas opuestas de temperatura y humedad relativa mostraron similar fluctuación como los encontrados en Selva Baja; sin embargo, el rango de las escalas fue más pequeño, posiblemente a causa de mejor combinación atmosférica facilitada por el dosel más abierto en bosque de montaña elegido para el presente estudio. La estabilidad microclimática disminuyo con la distancia del suelo. El micro hábitat en la parte baja del tronco fue el más húmedo, más fresco y menos iluminado. La temperatura más alta y humedad relativa mas baja fueron registradas en la media copa exterior, cercanamente seguido por la periferia de la copa mas irradiada. La temperatura sobre el dosel permaneció más fresco durante el día que la misma copa del árbol. El promedio de horario de la temperatura mas bajo fue registrado en la media copa, causado por el rápido enfriamiento radiativo en la noche. El aire sobre el dosel fue mas caliente en la noche como en cualquier micro-hábitat en el árbol.

En el estudio se encontró 27 especies de briofitas (5 musgos, 22 hepáticas) que no eran citados en el Perú. Las recomendaciones para metodología en estudios futuros de briofitas en los bosques de montaña baja peruana, son incluidas en el presente informe. Futuros estudios deben suceder paralelos a los esfuerzos concertados para la concientización de la población sobre la importancia ecológica de las briofitas, particularmente en los bosques nublados.

Acknowledgments

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The present study was inspired by Damien Catchpole and his study of vascular epiphytes in a *Ficus* sp. on the slopes of the Yanachaga-Chemillén Range, Peru. He provided much advice and facilitated many aspects of the study and home life in Oxapampa. Also, a thank you to Karen Richards, whose love of nature has always been and will continue to be an inspiration.

Much logistical support was provided by the Instituto Nacional de Recursos Naturales (INRENA). Co-operation of the staff at the Oxapampa office headed by Eduardo De la Cadena is much appreciated. Access to the facilities of the Missouri Botanical Garden Selva Central branch was invaluable. The staff, particularly Rodolfo Vasquez Martinez, his partner Rocio Rojas and Abel Monteagudo made me feel very welcome. I would also like to thank Percy Summers at Pro-Pachitea and the Fundación Peruana para la Conservación de la Naturaleza (Pro-Naturaleza) for their logistical support. A special thanks to Assoc. Prof Carlos Llerena Pinto who assisted with student visa requirements.

The volume of taxonomic literature that was necessary to complete the present study is staggering. Majority of it had to arrive in electronic format to this corner of the Amazon basin. I would like to thank the University and the library and document delivery staff, for their assistance. Prof. Rob Gradstein provided some key literature, as did Rod Seppelt, who also donated his time to demonstrate some laboratory techniques.

Bryologist are rare anywhere and especially so in Peru. A special thank you to Jasmin Opisso Mejia at the Museo de la Historia Natural in Lima, who gave up much time and provided the expertise necessary to clarify many doubts and verify the moss identifications.

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Chapter 1. Introduction

> *The "tropics" are not a plot of convenient forest in Costa Rica; they are an enormous realm of patchiness, and any theoretical thinking based on presumed general properties is bound to become an in-group exercise in short-lived futility.*
>
> - Paulo E. Vanzolini

The Neotropics are home to nearly 4000 bryophyte species or one third of the world's population (Gradstein *et al.*, 2001a). This disproportionate diversity, also recorded for vascular species, is higher than found in tropical Africa or Australasia and may be a consequence of the extremely broad range of habitats afforded by an altitudinal and climatic gradient stretching from the humid lowland Amazonia to the glaciated peaks of Huascaran (6768 m) and the dry Pacific slopes of the tropical Central Andes. Of the 595 bryophyte genera in 120 families, 80 moss and 50 hepatic genera are endemic to tropical America, making it the world centre of generic endemism (Gradstein *et al.*, 2001a).

The tropical Andes have long been recognized as the jewel in the biodiversity crown of the Neotropics (Gentry, 1992b). The region boasts an estimated 800-900 hepatics (liverworts and hornworts) and 1200-1400 moss species (Gradstein *et al.*, 2001a). Most diverse moss families include Dicranaceae (gen. 34/190 sp.), Daltoniaceae (9/200), Pilotrichaceae (21/200), Grimmniaceae (8/50) and Pottiaceae (55/361), contribution of the latter two becoming greater in the dryer areas of the south. Hepatics in the tropical Andes are rich in Gondwana groups that reach their widest distribution in temperate Southern Hemisphere and reoccur at high elevations in the tropics. Lejeuneaceae is by far the most species rich hepatic family, with 70 genera and approximately 400 species. Other diverse families are Lepidoziaceae (16/110), Plagiochilaceae (4/112) and Jubulaceae (2/80).

Woody plant diversity decreases above 1500 m. However, bryophytes reach their peak species richness in upper montane cloud forests at 2500-3000 m, where cooler temperatures and high frequency of moisture bearing low cloud encourage luxuriant growth of this ectohydric group of plants (Gentry, 1992b; Gradstein, 1995; Gradstein *et al.*, 2001a). Tropical montane cloud forests occur between 1500-3300 m and in the Neotropics stretch over both the lower montane (1000/1400-2000/2500 m) and upper montane (2000/2500-3000/4000 m) rainforest types (Bruijnzeel and Proctor, 1995b; Gradstein *et al.*, 2001a). Population pressure is pushing more colonists into the Andean montane forests. Both lower montane and upper montane forests are being cleared for timber, charcoal production and conversion to pasture and agriculture. In the north, 90% of cloud forest has already been cleared (Doumenge *et al.*, 1995), while in the Central Andes, Young (1992a) identified the lower montane forest as historically at greatest risk of conversion, although data about the more recent trends are not easily available. Considering the area occupied by montane forest, they are being modified at a greater rate than the lowland forest of Amazonia. This statistic is even more alarming in the light of the greater species diversity in montane forests than in Amazonia. The Northern Andes is estimated to support 40,000 species of flowering plants in an area 20 times smaller than the Amazon basin, which supports an estimated 30,000 species (Henderson *et al.*, 1991).

Besides their considerable contribution to the overall biodiversity of the region, bryophytes also contribute to the hydrological and nutrient cycles of montane forests (Veneklaas *et al.*, 1990; Coxson and Nadkarni, 1995). Epiphyte branch cover in upper montane cloud forests can exceed 80%, with bryophytes heavily contributing to this value. Harvesting of horizontal precipitation by tropical montane cloud forests can contribute an additional 5-20% to the annual rainfall (Bruijnzeel and Proctor, 1995b), with this function particularly valuable during the dry season. Chang *et al*. (2002) have shown that bryophytes are efficient captors of fog. Their experiment, carried out in montane cloud forest in Taiwan, revealed that on average 0.63 g of water was deposited per gram of bryophyte dry weight per hour, translating to 0.17 mmh^{-1} on a stand scale or 36% of the bulk precipitation received in the study area for the period of study. Clark *et al.* (2005), in their study at Monteverde in Costa Rica found that bryophytes intercept and capture as

much as 50% of wet deposited inorganic nitrogen (NO^-_3). This has important consequences not just for the availability of this essential and very mobile nutrient in wet montane forests, but like the intercepted horizontal precipitation contribution to stream flow, impacts on ecological processes far removed from the stream headwaters (Burns, 2003; Luo *et al.*, 2007). Despite these apparent ecological services, bryophytes remain poorly studied in the Neotropics and particularly so in the Central Andes of Peru and Bolivia (Gradstein *et al.*, 2001a). There is a pressing need for bryophyte species inventories to provide baseline diversity data to assist in conservation planning and to provide a foundation for further investigations of species dynamics and function.

Most of the species in rainforests are epiphytes; only 20% of those are shade epiphytes restricted to the low light and very humid environment of the understorey in undisturbed rainforests (Gradstein *et al.*, 2001a). Variation in species abundance throughout a tree crown reflects the individual taxa tolerance limits of environmental parameters, as well as colonization and turnover dynamics (Proctor, 1981; Van Leerdam *et al.*, 1990). A gradient of temperature, relative humidity and availability of photosynthetically active radiation exists from the trunk base to the outer crown and crown centre to outer crown, creating a mosaic of microclimates. Many epiphyte studies have adopted the Johansson zonation system to divide a host into microclimatically distinct areas (Johansson, 1974; Van Leerdam *et al.*, 1990; Kelly *et al.*, 2004). Although bryophyte species are quite sensitive to climate and habitat characteristics, the geographic distribution of individual species in the Neotropics is much broader than that of vascular plants (Gradstein *et al.*, 2001a). Studies in tropical rainforests have shown that sampling of 3-5 trees may reveal up to 80% of the local bryoflora (Wolf, 1993a; Gradstein *et al.*, 1996; Gradstein *et al.*, 2003b).

1.1 History

Exploration of Andean bryophyte diversity begun a little over 200 years ago. The earliest collections were those by José Celestino Mutis in Colombia (1783-1808) as subjects of illustrations in the "Flora de la Real Expedición Botanica del Nuevo Reino de Granada", unfortunately not published until 1985. His collection, deposited in the herbarium of the

Madrid Botanical Garden, is of greater historical than scientific significance, but has resulted in some of the earliest illustrations of Andean bryophyte flora (Churchill and Linares, 1995).

The earliest collections with a scientific interest were made by Alexander von Humboldt and A. Bondand who collected a few moss and hepatic samples near Ibague during their expedition to Colombia in 1801 grad. There was nearly a 40 year gap before J. Goudout (1844-1845) among others continued the exploration of the new world. Perhaps the most important collections of the 19th century were those of A. Lindig (1859-1865) and J. Weir (1863-1864) in Colombia, W. Jameson in Ecuador, A. Moritz and W. Fender in Venezuela and R. Spruce who collected in the latter half of the century in Colombia, Ecuador and northern Peru (Hampe, 1847; Churchill and Linares, 1995). His *Hepticae et Andinae* is still considered a landmark along the path to the modern understanding of Andean bryophyte flora (Spruce, 1884-1885; Gradstein, 1995).

The 20th century saw more frequent participation by local botanists like H. Garcia (1934-74) and L. Uribe U. (1939-72), assisted by north Americans W. L. Steere (1942-45) and F. R. Fosberg (Churchill and Linares, 1995). T. Herzog's expedition to Bolivia in 1916 and 1920 greatly advanced the knowledge of the otherwise little investigated Bolivian bryophytes (Churchill and Linares, 1995; Gradstein, 1995). Descriptive and taxonomy focused studies continues into the latter half of the 20th century with important works in the Colombian Andes by H. Bischler (1964), R. M. Schuster in Venezuala (1978) and E. and P. Hedgewald in peru (1977), among others. More recent studies conducted under the umbrella of the Dutch-Colombian Ecoandes project (Gradstein, 1982; van Der Hammen and Ruiz, 1984) and the BRYOTROP project in northern Peru (Frey, 1987; Kürschner and Parolly, 1998) among others (Gradstein *et al.*, 1990) adopted a broader focus that included bryophyte ecology and phytosociology. Wolf's description of communities along an elevation gradient spanning between 1000 m and 4133 m in the Santa Rosa de Cabal range, Colombia (Wolf, 1993b; Wolf, 1993c), the work of Gradstein and associates in Monteverde, Costa Rica (Sillett *et al.*, 1995; Gradstein *et al.*, 2001b), and the altitudinal

transect of H. Kürschner and G. Parolly in northern Peru (280-3300 m) (1998) provide an invaluable insight into the ecology of bryophytes in montane habitats.

1.2 Objectives

This thesis presents the findings of a crown to ground epiphytic bryophyte survey conducted in a lower montane cloud forest on the eastern foothills of the Andes (Peruvian Yungas), Pasco, Parque Nacional Yanachaga-Chemillén. This is the first study of its kind in the Selva Central of Peru and one of few for Peru.

The objectives were to:

i) determine the size of a representative subsample for the forest type in the study area,

ii) characterise the microclimatic variation throughout a single tree host in lower montane rainforest,

iii) determine the diversity of epiphytic bryophytes on a single tree host in lower montane rainforest,

iv) identify environmental variables that may have the greatest influence on the distribution of individual species within a host crown in lower montane rainforest.

1.3 Structure of the thesis

A brief review of methodology applied in epiphytic bryophyte studies and results of a pilot study to determine the minimum subsample size are presented in chapter 2.

A description of the microclimatic variation throughout the tree host is provided in chapter 3.

The findings of a single tree epiphytic bryophyte survey are presented in chapter 4. This chapter also includes the description of four epiphytic bryophyte communities identified on the tree host.

Results of ordination species and environmental data are presented in chapter 5. A discussion about the ability of some of the examined variables to explain the observed species distribution is also included.

The concluding chapter 6, provides a summary of the major findings of the present study, suggests a sampling methodology for future epiphytic biodiversity studies in the lowland rainforest of the Yanachaga-Chemillén Range and identifies themes for potential future studies of bryophyte ecology Peru.

Chapter 2. Methods

2.1 Study area

The study was conducted in lower montane rain forest on the isolated Yanachaga-Chemillén Range forming the eastern flank of the Peruvian Andes, Department of Pasco, central Peru. The approximately north-east extending range is included in the Yanachaga-Chemillén National Park (120,000 ha) and includes lowland rainforest along its eastern border, grading into lower montane and upper montane rain forest. The altitudinal range of the park is 400-3800m, with the tallest peaks near the western extremity of the park.

The area is under the influence of a moist easterly air stream originating as the Atlantic trade winds in the east. The moist air, recharged by the passage over the central Amazon basin, is redirected to the south by the Andes (Killeen *et al.*, 2007). Orographic lifting results in locally high precipitation on the eastern flanks of the Andes, including the Yanachaga-Chemillén Range. The area experiences a pronounced dry season between April and September (Fig. 2). Low cloud is common throughout the year. Hillsides are steep (20-60˚) and landslides common, even in undisturbed forest.

The study site was located at 2400 m a.s.l. on the leeward slope of the range, near its western extremity (10.32 S, 75.21 W). Mean annual precipitation is 2703 mm and mean annual temperature is 13.7˚C [1]. Expected annual levels of photosynthetically active radiation and mean annual relative humidity are 23.28 kmol.m-2.yr-1 and 93.4%.

The emergent stratum (to 38 m) of the surrounding forest is dominated by *Cedrela montana*. Co-dominant species form a broken canopy of 20-25 m and include *Nectaria reticulate*, *Ficus gigantosyce*, G*uarea kunthiana*, *Ruage pubescens*, *Croton* and *Weinmannia* species. The understorey includes small trees and shrubs in the families Ericaceae, Gesneriaceae, Melastomataceae, Piperaceae and Rubiaceae. Tree ferns in the

[1] Climate data for the site was recorded since 2003 and is provided here courtesy of Damien Catchpole, UTAS. Expected PAR is the above canopy value calculated from a hemispherical image.

genera *Alsophila*, *Cyathea* and *Dicksonia* are common. Most tree and shrub stems are covered with bryophytes. Vascular epiphytes are numerically dominated by Orchidaceae (Catchpole, 2004). Species in families Araceae, Bromeliaceae, Dryopteridaceae also abound in the crowns (Fig. 1).

Fig. 1 Lower montane rainforest near the study "El Cedro" site at 2400 m.

The site has been selectively logged for *Cedrela montana* and *Podocarpus oleifolius* up to some 20 years ago. However, species richness of the community remains quite high. A complementary study of a 1 ha plot including the site of the current study found 134 woody species among 516 individuals with diameters greater than 0.1m (Requena Rojas, 2007); 195 species of vascular epiphytes were found in a nearby emergent *Ficus* sp. (Catchpole and Kirkpatrick, 2005).

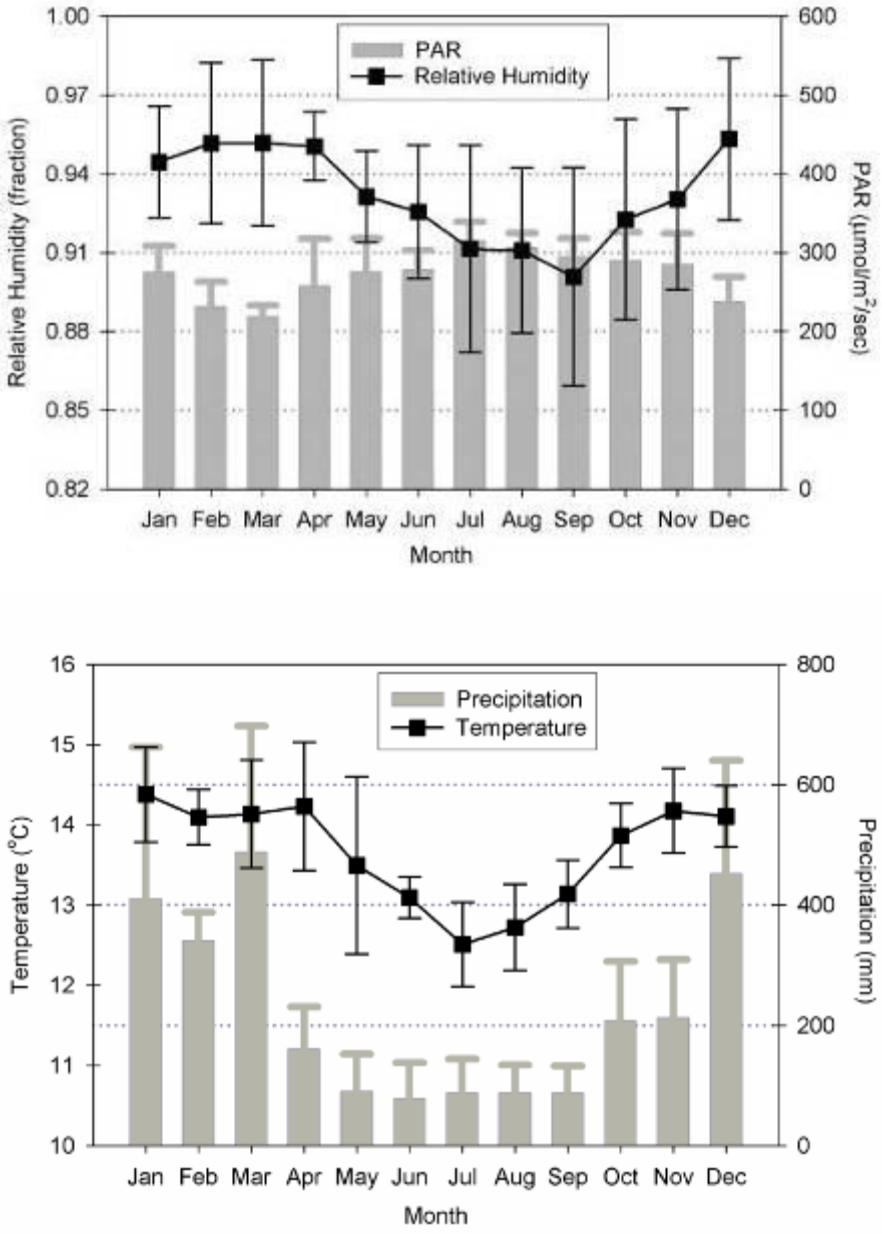


Fig. 2 Mean monthly relative humidity, photosynthetically active radiation (PAR) , precipitation and temperature at "El Cedro", Yanachaga-Chemillén National Park, Peru (Catchpole *et al.*, In press).

2.2 Methodology review

It is difficult to compare the findings of most species diversity studies, not just because of the variation in sampling technique, but also due to the myriad of methodologies employed to obtain a "representative" sample of the true populations. The techniques vary greatly in their emphasis on quantitative accuracy and species capture, potentially leading to contradictory findings about the characteristics of a community, dependent on the technique and method used (Newmaster *et al.*, 2005).

Relevé sampling intensively inspects large areas. Its emphasis is on gathering species presence information (Braun-Blanquet, 1932; Newmaster *et al.*, 2005). Floristic habitat sampling adopts a slightly more rigorous method, more attuned to the accepted close relationship between bryophyte species and microhabitat characteristics (Bouchard *et al.*, 1978; Proctor, 1981), despite their overall broad geographic ranges (Gradstein *et al.*, 2001a). Some studies have used a list of microhabitats (rocks, logs, cliff crevice, stream side etc.) present within a mesohabitat (type of forest or landscape unit) to further formalise the sampling process (Vitt and Belland, 1997; Newmaster *et al.*, 2005). A survey may be considered adequate when no singleton species remain. Plot sampling includes a vast array of methodologies, from pin frame samples to area and time limited sampling. Tokeshi (1993) advises that at least 10 samples should be collected to facilitate sound statistical analysis. Different plot shapes have been used: square, rectangular, strip and line plots, each shown to differently capture within landscape habitat heterogeneity (McCune and Lesica, 1992; Gradstein *et al.*, 1996; Eldridge *et al.*, 2003). The opportunity to mix and match these approaches is endless.

There is a positive relationship between the overall species richness and sample size (Magurran, 2004). Large single areas have been shown to better capture species richness than plot samples of an equivalent area (McCune, 1988; McCune and Lesica, 1992; Archaux *et al.*, 2007). However, the more extensive methodologies are criticised for their poor quantitative accuracy (species abundance) (Archaux *et al.*, 2007; McCune and Lesica, 1992). Plot samples provide more accurate and precise species abundance measures that are more easily tested statistically and applied to compare different

communities. However, in there lays a paradox as many of the species richness descriptors rely on information about the rare species that may be overlooked by plot sampling methodologies (Newmaster and Bell, 2002).[2] In short, the negative relationship between species capture and quantitative accuracy seems to grade from large single samples being best at revealing species richness, to intermediate performance of elongate plot samples, with small sample areas providing most reliable abundance measures (McCune and Lesica, 1992; Newmaster *et al.*, 2005; Archaux *et al.*, 2007). One needs to be careful when interpreting findings of other studies, but also be clear about the purpose when designing a study and be aware of the shortcomings of the adopted sampling methodology.

Difficulties in comparing the findings from multiple studies have long been recognised. A group of prominent ecologist has been working on a standardised methodology for investigation of various components of epiphytic species diversity in tropical environments (Gradstein *et al.*, 1996). The latest "protocol for rapid and representative sampling of vascular and non-vascular epiphyte diversity of tropical rain forests" has been presented by Gradstein *et al.* (2003b). Based on numerous studies, they suggest that the minimum sample size for vascular epiphytes does not need to be large. Sampling of just eight trees and surrounding 20 x 20 m plots revealed 80% of the estimated total vascular species richness for 1 ha of a Bolivian montane forest (Krömer, 2003). The minimum sample size for non-vascular epiphytes is even smaller. Sampling of 3-5 trees identified 75-80% of total bryophyte diversity of a tropical forest (Acebey *et al.*, 2003). For epiphytic bryophyte diversity studies, Gradstein *et al.* (2003) suggest sampling just 5 trees and woody vegetation within a 20 x 20 m plot around each tree. Sampling of trees should be conducted in five Johansson (1974) zones using 5 subsamples in each zone[3]. The

[2] Information on the infrequent species is necessary to reveal the mode of the parametric lognormal species abundance distribution, frequently hidden by the "veil line" in incomplete surveys. Magurran AE (2004) 'Measuring biological diversity.' (Blackwell) . Popular non-parametric estimators of Anne Chao, like the Chao1, Chao2, ACE and ICE all rely on rare species data to derive their estimates of species richness. Chao A (1984) Non-parametric estimation of the number of classes in a population. *Scandinavian Journal of Statistics* **11**, 265-270.; Chao A, Hwang WH, Chen YC, Kuo CY (2000) Estimating the number of shared species in two communities. *Stat. Sinica* **10**, 227-246.

2 Johansson zones reflect gradients in climatic and an array of habitat parameters that influence species presence. Temperature, light and especially moisture availability were identified as important. Crown architecture, bark acidity and texture and age also influence habitat preferences of epiphytic species. Barkman JJ (1958) 'Phytosociology and ecology of cryptogamic epiphytes.' (Assen)

subsample size in zones 1-3 should be randomly positioned by cardinal direction and measure 300 x 200 mm. Plots on branches in zones 4-5 should be 600 mm long, 3 located on the upper and two on the lower branch surface, with total area dependent on branch size.

The lack of basic species presence data for this region and Peru in general, and very limited resources for this project force the adoption of a species capture focus. Similar to other groups of plants, bryophyte species richness varies between different landscape units or forest types. In the Neotropics, bryophyte diversity increases with elevation and peaks in the cloud forests of the upper montane belt at 2500-3000 m before dropping again in sub-alpine formations (Wolf, 1995; Gradstein *et al.*, 2001a). Is it likely that one sampling method can adequately capture species diversity across this gradient of species richness and the mosaic of habitats? From the introduction above, it is clear that more extensive studies yield more complete species lists and some type of stratification by microhabitat of the sampling effort is desirable to most efficiently use limited resources.

But, how large does a subsample need to be to capture at least 75% of the epiphytic bryophyte species richness in each section of a tree, in lower montane rainforest on the Yanachaga-Chemillén Range, Peru?

2.3 Minimum subsample study

2.3.1 Methods

- Two mature canopy codominant trees (Table 1) were selected on the following criteria:

i) apparent richness in epiphytic bryophytes,

ii) contrasting bark type and crown structure,

iii) crown structure conducive to safe access with rope an harness techniques.

Table 1. Subsample study tree details, including location of zone samples.

Family Species	Hgt (m)	Dia. (m)*	Notes	Zone height / diameter (m) 1	2	3	4	5
Euphorbiaceae *Alchornea* sp.	25.5	0.42	Complex, dense crown of strong upright young leaders amongst older, previously broken ones. Young bark smooth, older shallowly fissured with prominent lenticels.	1.5 / 0.42	10/ 0.37	19.5/ 0.23	22/ 0.07	24.5/ 0.03
Euphorbiaceae *Croton* sp.	29.7	0.51	Open decurrent crown, home to a pair of nightjars. Bark smooth throughout. Sap, locally known as "sangre de grado" (blood of the dragon) has medicinal uses as antiseptic on wounds, for fighting stomach infections and ulcers.	1.5 / 0.51	9/ 0.25	20.7/ 0.19	25.5/ 0.09	28.2/ 0.03

* - Trunk diameter measured at 1.3m (DBH)

- A contiguous grid of 6 subsamples of 100 x 100 mm was established in each zone in the two trees. In zones 1-3, the collective sample size was 300 x 200 mm and 600 mm of branch length in zones 4-5. Where possible, the sampling grid was placed across the trunk or branches in zone 3 to reduce redundancy of microsites with similar light characteristics. Cardinal aspect of the collections was not considered. Collections were made on the 19th and 20th of May, 2006.

- The crown was accessed with single rope and arborist techniques (Perry, 1978; Dial, 1994).

- Morphospecies within each subsample were identified using dissecting and compound microscopes.

- The morphospecies data for each sample and across zones in the two trees was examined using sample based rarefaction curves (species accumulation curves) generated in EstimateS programme (Colwell, 2005). The curves were calculated without sample replacement.

- The relationship between the number of morphospecies recorded in entire and reduced samples was examined with the aid of MINITAB v.14 (14.12.0) programme (Minitab Inc., 2000)

2.3.2 Results

A total of 99 morphospecies (72 hepatics and 27 moss sp.) were found on the *Alchornea* sp. and *Croton* sp., 81 and 65 morphospecies respectively. The *Alchornea* sp. shared the same number of morphospecies in zone 4 with the *Croton* sp., but had fewer in zone 2 (Fig. 3). One subsample from zone 3 of the *Alchorea* sp. included 35 morphospecies, while average number across all subsamples was 15.6.

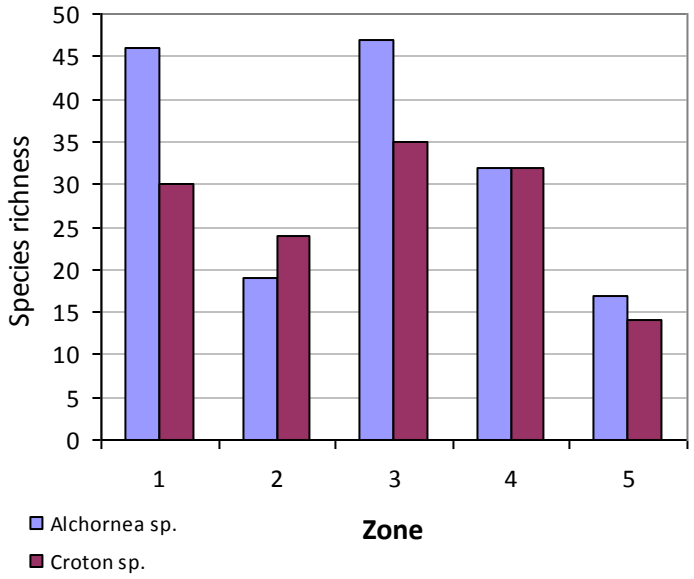


Fig. 3 Zone species richness in the *Alchornea* sp. and *Croton* sp. hosts.

Inspection of the species accumulation curves generated for all samples revealed a common trend. 75-85.5% of the known species richness included in each sample was collected in just 3 subsamples (Table 2). Pooled subsamples and morphospecies across zones showed a similar trend (Table 3). An example of a typical sample rarefaction curve for samples and pooled zone data from both trees is presented in Fig. 4.

Table 2. Proportion of a known sample species population revealed by 1 to 6 subsamples.

	1.1	1.2	2.1	2.2	3.1	3.2	4.1	4.2	5.1	5.2
1	58.70	52.23	50.00	49.29	54.26	50.94	54.69	48.44	51.00	46.43
2	73.76	70.43	68.42	67.50	72.77	69.34	74.78	69.16	68.65	62.86
3	83.59	81.33	79.74	79.17	83.19	80.43	85.47	81.25	79.41	75.00
4	90.72	89.33	88.05	87.79	90.36	88.37	91.88	88.97	87.47	84.79
5	96.02	95.57	94.74	94.46	95.74	94.77	96.34	94.78	94.12	92.86
6	100	100	100	100	100	100	100	100	100	100

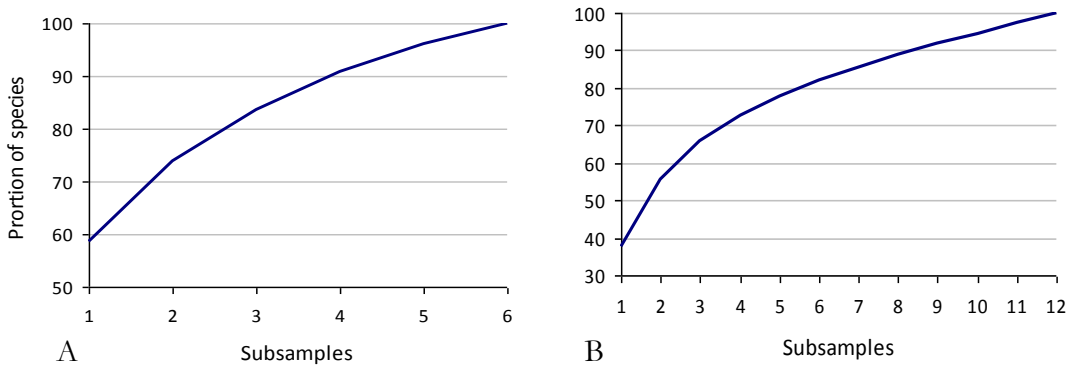


Fig. 4 A) *Alchornea* sp. zone 1 species rarefaction as proportion of species from a known population; B) zone 4 species rarefaction curve (pooled data from *Alchornea* sp. and *Croton* sp. individuals).

Table 3. Proportion of a known zone species population revealed by 1 to 12 subsamples (pooled data from *Alchornea* sp. and *Croton* sp. individuals).

	Zone				
	1	**2**	**3**	**4**	**5**
1	37.42	31.38	36.73	37.50	32.96
2	55.07	48.76	55.97	55.43	47.48
3	66.25	60.35	67.80	65.89	57.26
4	73.96	68.85	75.73	72.82	64.70
5	79.70	75.47	81.41	77.95	70.87
6	84.26	80.79	85.71	82.09	76.26
7	88.02	85.26	89.12	85.64	81.13
8	91.18	89.09	91.93	88.84	85.52
9	93.89	92.38	94.32	91.82	89.57
10	96.23	95.26	96.42	94.64	93.26
11	98.25	97.79	98.31	97.34	96.74
12	100	100	100	100	100

The ranking of total number of observed species was strongly negatively correlated with the proportion of species captured with 3 subsamples (Fig. 5)

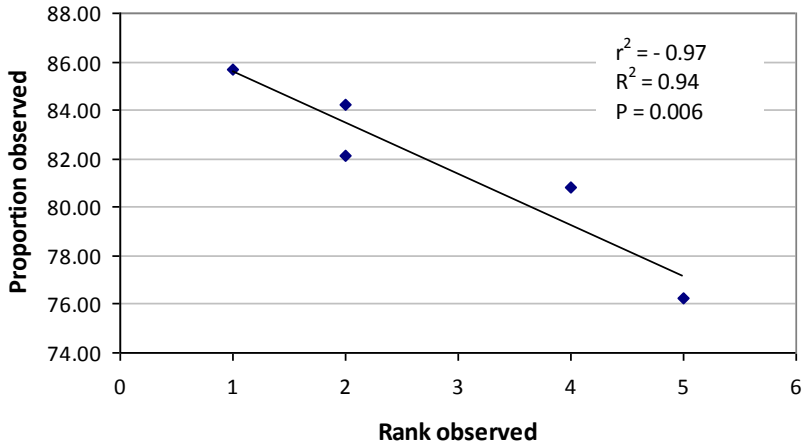


Fig. 5 Plot of rank of observed species in 5 Johansson zones (sample area of 0.06 m^2) and proportion of observed species captured in 0.03 m^2 in each zone.

2.3.3 Discussion

The effort required to process the samples from this small pilot study was substantial. On average, each subsample took one day to separate into morphospecies. The time required to complete this study certainly reflects the inexperience of the author with tropical taxa, but also highlights the species richness of the local bryophyte community. An average of 15.6 morphospecies was identified in each square decimetre and 35 were present in one subsample from zone 3 of the *Alchorea* sp.

The samples consisted of interwoven mats of predominantly weft and mat growth-forms in zones 1-4, giving way to tightly adpressed mats and individual wefts in zone 5. A large proportion of the species are less than 1 mm across the leafy stems. The advice of Gradstein *et al.* (2003b) to separate individual species and attempt their identification under field conditions does not seem practical. Many morphologically similar hepatic taxa, particularly among the Lejeuneaceae, and moss species can only be separated

following close examination of their anatomy and cytology, to say nothing of the morphologic plasticity within taxa.

The EstimateS programme used to produce the rarefaction curves and others, like PC-ORD, do not consider the spatial arrangement of samples. Samples are assumed to be non-contiguous (Scheiner, 2003). The worst case of subsample distribution under the present grid system (3 x 2 subsamples) would be two adjacent subsamples and one separated by 100 mm, a feature that needs to be considered when designing a larger study.

The ranking of the proportion of species captured by three subsamples within each zone may reflect the overall zone species density (Table 3). The strong relationship between rate of capture and overall species richness supports this hypothesis and justifies the doubt expressed above about the efficiency of a single sampling method to adequately represent the varying levels of species richness across different forest types (Fig. 5). Lennon *et al.* (2001) found that local richness gradients had a large impact on beat diversity estimates and others observed that species turn over is negatively related to species richness of an area (Magurran, 2004). The method suggested by Gradstein *et al.* (2003) is likely to underestimate the specie richness of less diverse assemblages, exaggerating the contrast between those and species rich areas.

Gradstein (1995) used the number of hepatic epiphytes found on four trees to compare hepatic richness in different tropical forest types. He found that the average number of species in lower montane forest was 46 and in upper montane forest 86. This pilot study conducted in the upper reaches of the lower montane belt, despite its very small sample size, found 72 hepatics on just two trees. Could the bryophyte diversity of the forest on the Yanachaga-Chemillén Range be greater than average?

2.3.4. Conclusion

The effort required to sample and process epiphytic bryophyte samples is montane rainforest is substantial. This study demonstrated that a subsample of 0.06 m^2 is

unnecessarily large in lower montane cloud forest at 2400 m. on the Yanachaga-Chemillén Range. Samples of half that size (0.03 m^2) can capture 75% of the microsite species richness. Smaller, but more numerous subsamples strategically placed across niche rich habitats are likely to be more efficient and produce more accurate species richness estimates than few large randomly placed samples. This is a contradictory finding to the general belief that large samples are better at species capture than many randomly placed small quadrats (McCune and Lesica, 1992; Archaux *et al.*, 2007). The approach suggested here is not dissimilar to the modified floristic habitat sampling stratified by microhabitat as applied by Newmaster *et al.* (2004).

2.4 Single tree study design and methods

2.4.1 The host

A mature canopy co-dominant *Weinmannia* sp. was chosen as the subject of the single tree bryophyte epiphyte survey (species name was not determined, despite expert assistance). *Weinmannia* L., (Cunoniaceae R.Br.) is a genus of approximately 150 species of trees and shrubs distributed throughout the montane regions of the Neotropics. Forty-one species have been recorded for Peru (Pennington *et al.*, 2004).

The tree was chosen for its unremarkable stature, average volume of epiphytes and importantly, an architecture that promised access to the outer reaches of the crown. The *Weinmannia*, unaffectionately called Tree 3, became Mannie over the course of the study. It was 25.5 m high and its single trunk DBH (at 1.3 m) was 0.7 m. The crown had a diameter of 10-12 m.

The tree was growing on a narrow shelf of a 40˚ sloping hillside, a north-eastern escarpment of a narrow valley. The dense understorey occluded the trunk on the eastern, slope side, but was thinner above 2 m. on the south-western side, leaving the trunk exposed to the late afternoon sun. The shallowly buttressed lower trunk had a lean of approximately 4˚ into the valley, above a noisy stream some 30m below. Mid and upper trunk continued to curve away from the bank. At 14.5 m., below the main bifurcation, the trunk had a lean of 12˚. Its base and eastern side was densely covered with bryophytes.

The western side was very sparsely covered and had large, apparently bare areas coloured by a patchwork of crustose lichens. It appeared obvious that the western side of the trunk was exposed to the afternoon sun.

The fine, sparse crown was supported by two main leading branches spreading on along an approximately north-south axis. Their bryophyte-mat covered bases had an approximate diameter of 200 mm. Long and sinewy, the leaders rose some 11 m to the twiggy pinnate leafed branch tips. Scaffold branches were few and distantly spaced. The crown supported surprisingly few large bromeliads and the bryophyte mats were only occasionally dotted with small orchid species. In the course of the study, a troop of monkeys occasionally strolled through the nearby tree tops, humming birds were common, but perhaps the most memorable was the visit by an Andean bear in a neighbouring crown, and of course, the mosquitos!

2.4.2 Crown stratification and access

Stratification of the trunk and crown following Johansson (1974) is well established among the canopy ecology researchers and will continue to be used in this study. It is customary to divide the trunk into the base (generally the first two meters), the lower, often more humid trunk section and the dryer upper trunk. As indicated above, the trunk had a pronounced dry side – a common feature of trees in montane forest on steep slopes. The division of the trunk and crown for the present study is illustrated in Figure 6.

Socializing in a *Cedrella montana* emergent.

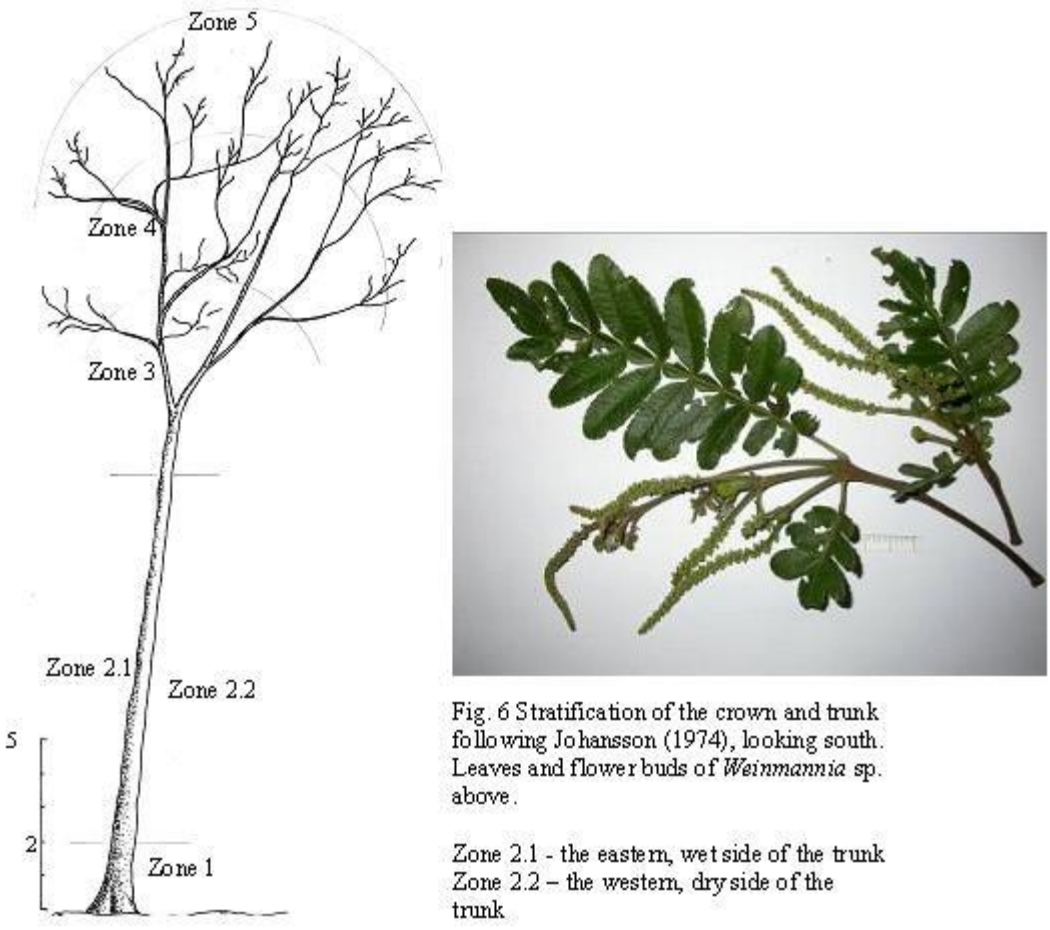


Fig. 6 Stratification of the crown and trunk following Johansson (1974), looking south. Leaves and flower buds of *Weinmannia* sp. above.

Zone 2.1 - the eastern, wet side of the trunk
Zone 2.2 – the western, dry side of the trunk

The crown was accessed with single rope and arborist techniques outlined by Perry (1978), Dial and Toblin (1994) and Jepson (2000). The structure of the host permitted access to within 1 m of most branch tips.

2.4.3 Floristic sampling and identification.

Epiphyte sampling, conducted *in situ*, was stratified by Johansson zone. Choice of subsample location was guided by accessibility and the apparent microhabitat variation. Ten subsamples were collected from each zone. Subsamples of 0.03 m^2 (100 x 300 mm) were used in zones 1-3. In zones 4-5, a 300 mm length of branch was used as the subsampling unit, with area dependent on branch size. Due to the overwhelming influence

of the local topography, cardinal direction was not considered during data collection. Direct sunlight was blocked by the steep hillside to the north during a large portion of the day.

Each subsample was placed in a paper bag and processes under both dissecting and compound microscopes in the comfort of a laboratory. Species identification to genus heavily relied on the excellent guide by Gradstein *et al.* (2001) for both hepatics (here including both liverworts and hornworts) and mosses. A list of taxonomic literature is provided in Appendix I. It was necessary to consult literature in Spanish, French, German and English. The multilingual glossary for bryology, published by the Missouri Botanical Garden proved invaluable (Magill, 1990). Identification of moss species was kindly confirmed by Jasmin Alexandra Opisso Mejia, a bryologist at the Museo de la Historia Natural, Lima. Unfortunately, no expert advice was available to confirm the hepatic determinations.

A voucher collection was deposited at the Selva Central Herbarium (HOXA) of the Missouri Botanical Garden.

2.4.4 Temperature and relative humidity

Fig. 7 Shielded LogTag temperature and relative humidity logger in zone 4 of the *Weinmannia* sp. host.

Both temperature and humidity data were collected with LogTag HAXO-8 card loggers (MicroDAQ.com). The loggers have a temperature resolution greater than 0.1˚C and 0.1% relative humidity. The sensors were shielded with custom built 6 plate radiation shields (Fig 7). The loggers were suspended from custom built metal brackets attached to branches and trunk. The sensor was placed within 100 mm of the tree surface, in close proximity to the epiphyte collection sites. Another shielded LogTag logger was placed on a meteorological tower, some 50 m to the north. The

top of the tower and logger position was approximately 6 m above the forest canopy. The loggers recorded temperature and relative humidity every 10 minutes.

Readings were taken between 15/10/06 and 29/11/06, corresponding to the transition period between the dry and wet seasons in the Selva Central of Peru. In each zone, one fixed and two roving loggers were used. The roving loggers were moved every 9 days to a close proximity of one of 9 remaining epiphyte collection sites within each zone. A full temperature and relative humidity data set for each sampling site was derived (using zone 1 as example):

i) regression of fixed logger in zone 1 (site 1) on mobile logger 1 (site 2) for period 1,

ii) the regression model from above was applied to the complete study readings for the fixed logger in zone 1 (x) to obtain expected complete study period values for site 2 (y).

Relocation of the loggers took some hours. To allow for reaclimatisation of the shifted loggers, a full day (day nine) was removed from the climate data.

2.4.5 PAR

Radiation data was obtained from a hemispherical image taken with a NIKON 4500 Coolpix digital camera (3.87 million pixels) and processed by the hemispherical image analysis programme HemiView (Delta-T Devices Ltd., 2001).

The photos were taken with a FISHEYE 1 setting, sharpening function set to HIGH, exposure set to -2.0 and using the 10 second timer to reduce jitter. Images were stored at the highest available resolution. The camera was mounted on a custom built aluminium staff fitted with perpendicular horizontal levels. The photographs were taken either early in the morning or late in the afternoon to reduce reflections from foliage and bark. Despite this, a number of images had to be adjusted to remove light coloured objects from below the image horizon.[4]

[4] The site is surrounded by ridges and it is those that define the horizon.

The solar model used in the calculation of incoming radiation by the HemiView programme was calculated from real site data (Catchpole, 2004); 2900 μmol $m^{-2}s^{-1}$, yearly average transmissivity is 0.39, diffuse proportion is 0.57

2.4.6 Statistical analyses

- Climatic and radiation data were examined and tested with various procedures within the MINITAB v.14 (14.12.0) programme (Minitab Inc., 2000).
    - the Kruskal-Wallis test was used to examine the similarity between medians,
    - the Mann-Whitney pair comparison was used to identify similarity between subsets of zone data.
- EstimateS 7.5.0 programme (Colwell, 2005) was employed to:
    - generate species accumulation curves with 100 randomisations of the sample data without replacement,
    - generate species richness estimates and species richness indices,
    - assess similarity in species composition between sites and generate similarity indices.

- PC-ORD v. 4.27 programme (McCune and Mefford, 1999) was used to:
    - generate classification dendrograms,

  Normal classification was performed with species incidence data to reveal the similarity between sites. Continuity in community composition was examined with an inverse classification of species using sum incidence data. Species with less than 2% frequency were excluded from the analysis (95 species used). Both analyses were performed without any further transformation of the data.

  A number of distance measures and types of clustering were examined prior to choosing the most likely outcome for the classification.

- perform indicator species analysis,

The analysis employed the method of Dufrene and Legendre (1997).

- perform principal components analysis (PCA) on environmental data,
- perform non-metric multi-dimensional scaling (NMS) ordination,

The analyses performed 40 runs of real data, 50 runs of randomised data. NMS ordination was performed on a reduced species set (95 species, species with overall frequency of < 2% were excluded) and a reduced number of environmental variables (7 and 6 variables).

Chapter 3. Microclimate

3.1 Background

Much has already been published about climatic variation in rainforests (Richards, 1952; Walter, 1971). In contrast, few studies to date have investigated the microclimatic gradients within tree crowns and fewer still have taken place in montane rainforests (Kira and Yoda, 1989; Freiberg, 1997; Szarzynski and Anhuf, 2001; Cardelus and Chazdon, 2005; Catchpole *et al.*, 2005). Sensitivity of bryophytes to variation of light, temperature, moisture availability, substrate acidity among other factors is well accepted (Barkman, 1958; Proctor, 1981) and the distributional variation of species and growth-forms throughout tree crowns has not gone unnoticed (Van Leerdam *et al.*, 1990; Wolf, 1994). Intra crown climatic variation could influence the physiology of both tree hosts and epiphytes and may assist in forming hypotheses about the observed patterns of epiphyte species distribution.

Temperature and relative humid generally follow opposing gradients from the ground to the crown periphery (Kira and Yoda, 1989; Freiberg, 1997). In rainforests, coolest temperatures generally occur near the ground. This coincides with the highest light interception levels; on average, as little as 1% of the above canopy radiation reaches the rainforest floor (Kira and Yoda, 1989). Highest temperatures and lowest humidity occur in the outer crown, with corresponding low light interception.

The general pattern of diurnal fluctuation of temperature and relative humidity is much more complex. As the crown heats up during the day, the warmer air in the crown is decoupled from the cooler air in the understorey and turbulently mixes with the boundary layer above (Szarzynski and Anhuf, 2001). The rise of temperature and drop in relative humidity is much more pronounced in the outer crown than near ground level. At night, radiative cooling at the top of tree crowns results in lower temperatures there than near the ground, where loss of long-wave radiation is reduced by the overtopping canopy (Freiberg, 1997; Szarzynski and Anhuf, 2001). There is little variation in humidity throughout the profile.

A contrasting diurnal pattern was found by Catchpole in his study conducted in a *Ficus* sp. in close proximity to the present study site (Catchpole *et al.*, 2005). There, the lowest nightly temperatures occurred near the ground and above the crown, and maxima in the crown. Day maxima were reached above the crown and minima in the mid-crown. He attributes the observed climatic pattern to the characteristics of vascular epiphyte distribution and crown structure.

Epiphytes in tree crowns may be influenced by microclimatic parameters, but they themselves also modify the crown microclimate (Freiberg, 1997; Freiberg, 2001; Stuntz *et al.*, 2002). Temperature fluctuations immediately near branches were shown by Freiberg (1997, 2001) to be moderated by the presence of epiphytes and crown humus. The effect was strongest within 100 mm of the branch surface, with little difference beyond 0.75 m away from the branch (Freiberg 2001). Elevated relative humidity and lower temperatures associated with the moisture holding capacity of the epiphytic material and canopy humus not only have the potential to reduce evapotranspiration at microsites near epiphyte clumps, but also can significantly lower the moisture loss from their host (Stuntz *et al.*, 2002).

The objective of the present study was to describe the temperature, relative humidity and radiation characteristics of a canopy co-dominant crown in lower montane rainforest, during the transition period between dry and wet seasons in the Selva Central, Peru.

3.2 Results

Methods are presented in Chapter 2, section 2.4.

3.2.1 Temperature and relative humidity

Both temperature and relative humidity (RH) data collected from the crown were not normally distributed. RH data was strongly left skewed, while temperature data was right

skewed (Fig. 8). Neither of these data sets passed the Anderson-Darling or the Ryan-Joiner normality tests.

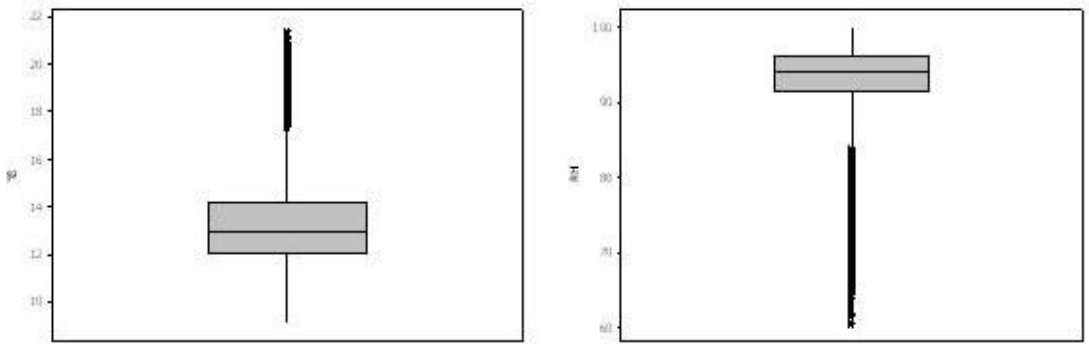


Fig. 8 Box plots of crown temperature (left) and relative humidity data (right) collected over a six week period (Oct-Nov) in a *Weinmaina* sp., lower montane forest, Peru.

The box indicates the interquartile range with a median line. The central axes represent the data range. The starred points in the range are unusual observations.

Highest and lowest temperature among all zone and above crown readings for the study was 20.75 ˚C in zone 5 and 9.1 ˚C shared by zones 3 and 5. RH extremes were recorded in zone 1 (100%) and zone 5 (60.59%).

The mean temperature and relative humidity within the crown over the study period was 13.3 ˚C (SD=1.82) and 93% (SD=5.25). The means above the crown for the same period were 13.5˚C (SD=1.69) and 87.8% (SD=4.76) (Fig. 9). The opposing gradients of mean temperature and for RH (between zones 1-4) were 0.41˚C and 8.3% respectively, disrupted by lower temperature and higher RH in zone 5.

Interquartile range (IQR) is less affected by outlying values and is considered by some to be a more accurate gauge of variation within a data set than the overall data range (Barmuta, L. 2005 pers. comm., lecturer, School of Zoology, UTAS). The greatest IQR in temperature was recorded in zone 5 (2.77˚C) and the lowest in zone 2.1 (1.22˚C). RH extremes in the IQR were provided by zones 5 (6.15%) and zone 1 (1.25%) (Fig. 10).

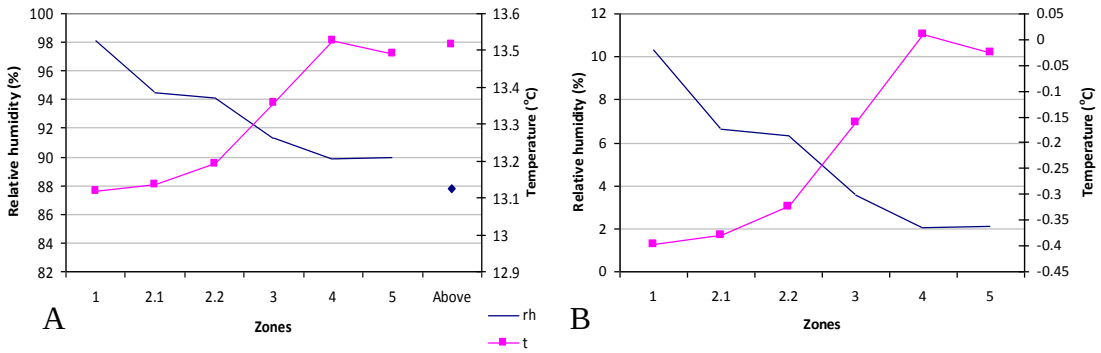


Fig. 9 A) Mean temperature and relative humidity in Johansson zones of the *Weinmannia* sp. host (Fig. 6) and above the forest canopy. B) The difference between the zone means and the above crown mean for temperature and relative humidity.

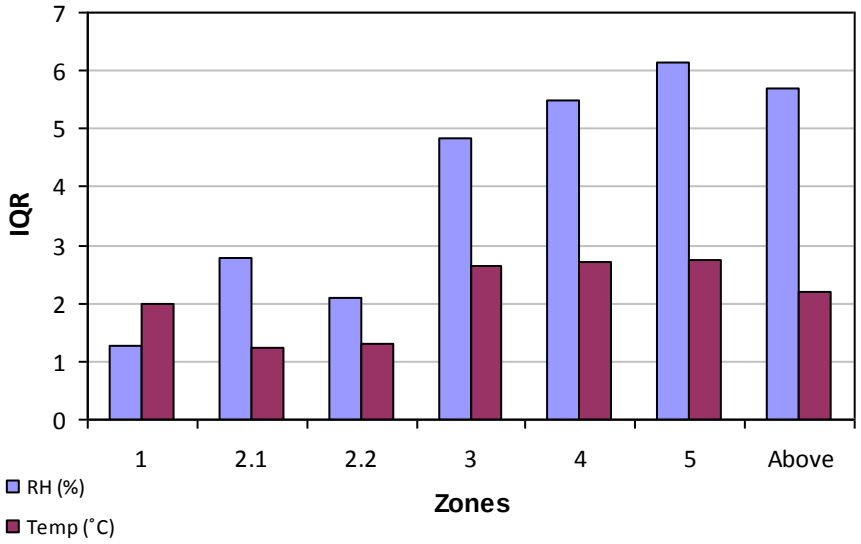


Fig. 10 Interquartile range of zone and above the canopy temperature and relative humidity data.

3.2.2 Radiation

All of the radiation associated parameters: visible sky (VisSky), leaf area index (LAI), total below radiation (TotBe), direct below radiation (DirBe) and diffuse below radiation (DifBe) had non-normal distributions, confirmed by both Anderson-Darling and Ryan-Joiner tests (Fig. 11).

As could be expected, the highest sample site VisSky proportion (0.46) and the lowest LAI (0.63) were recorded in zone 5, with contrasting values obtained near the ground in zone 1 (VisSky = 0.03, LAI = 5.56). These opposing gradients were also reflected by the zone means (Fig 12).

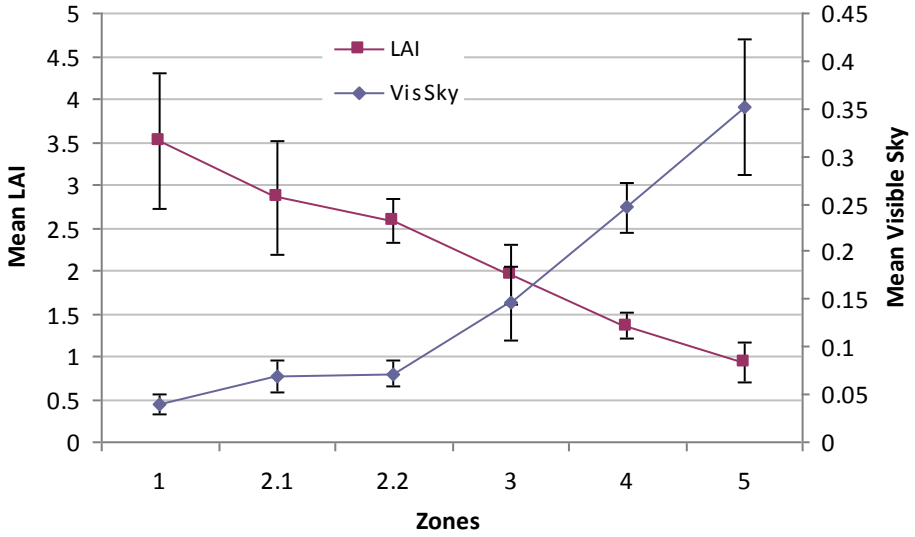


Fig. 12 Mean visible sky and LAI for Johansson zones and above the canopy.

The within zones range of values for these variable also had an opposing trend, with less variation recorded lower in the canopy for VisSky than among LAI values (Fig 11)

The different means and ranges of below radiation data recorded throughout the crown suggest the existence of a heterogeneous radiation environment within and between zones (Fig. 11 and 12)

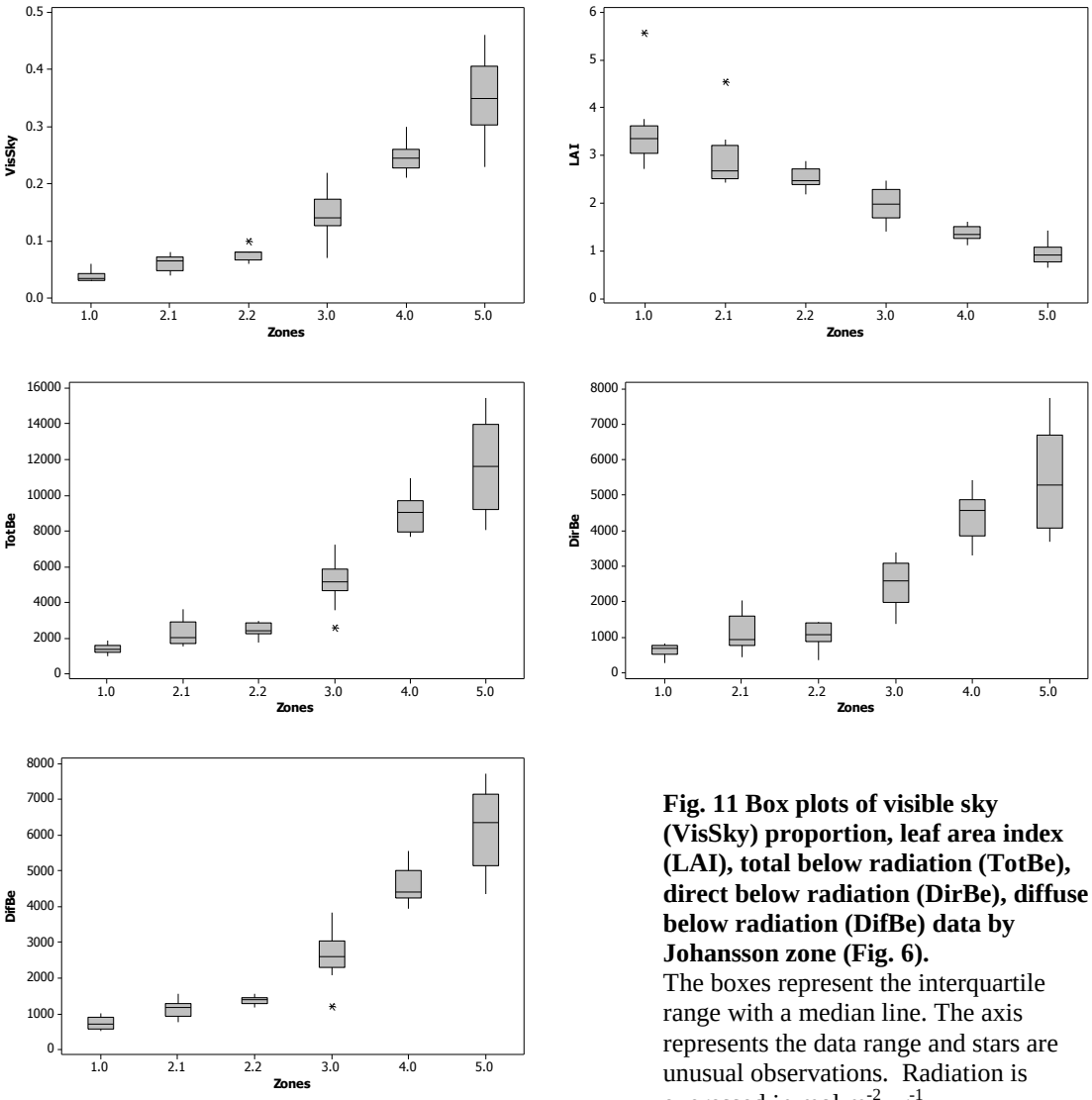


Fig. 11 Box plots of visible sky (VisSky) proportion, leaf area index (LAI), total below radiation (TotBe), direct below radiation (DirBe), diffuse below radiation (DifBe) data by Johansson zone (Fig. 6).
The boxes represent the interquartile range with a median line. The axis represents the data range and stars are unusual observations. Radiation is expressed in $mol.m^{-2}.yr^{-1}$.

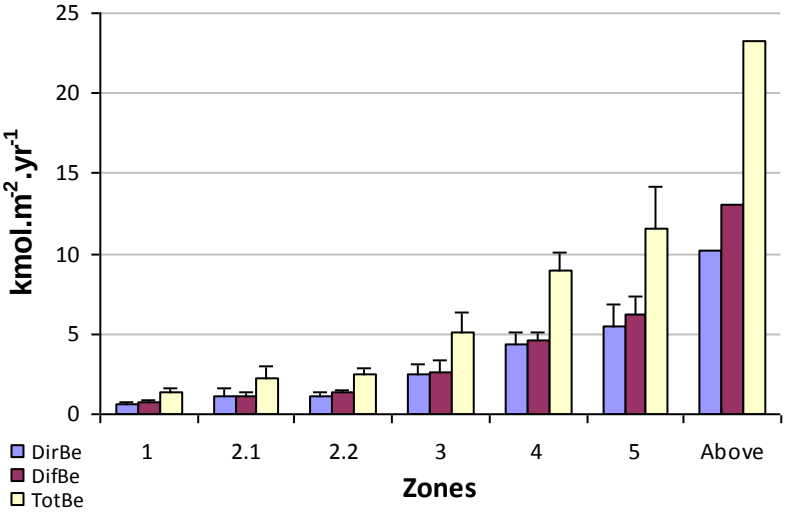


Fig. 13 Means in Johansson zones for total (TotBe), direct (DirBe), diffuse below crown radiation (DifBe) and above the canopy.

Mean TotBe for the *Weinmannia* sp. host (5293 mol.m^{-2}.yr^{-1}) amounted to just 22.7% of the total above canopy radiation (23.276 kmol.m^{-2}.yr^{-1}) (Fig. 13). The lowest IQR among the TotBe values was found in zone 2.2 (610 mol.m^{-2}.yr^{-1}), the exposed side of the trunk and the highest in zone 5 (4782 mol.m^{-2}.yr^{-1}). There was generally more variation in mid to upper crown than along the trunk (Fig. 11).

Both direct and diffuse fractions of below crown radiation followed a similar positive gradient to that of VisSky although the ratio between the two types of radiation varied among zones (Fig 14 and 15).

Zone 1, with a mean of 624.9 mol.m^{-2}.yr^{-1} had the least variation (IQR = 263.8 mol.m^{-2}.yr^{-1}) among the DirBe values recorded for the profile. The greatest IQR for this variable was observed in zone 5 (mean = 5433 mol.m^{-2}.yr^{-1}, IQR = 2628 mol.m^{-2}.yr^{-1}). Highest mean (1366.6 mol.m^{-2}.yr^{-1}) and lowest IQR (143.9 mol.m^{-2}.yr^{-1}) among the DifBe zone values was recorded in zone 2.2, with maxima for both mean (6187 mol.m^{-2}.yr^{-1}) and IQR (1998 mol.m^{-2}.yr^{-1}) provided by zone 5.

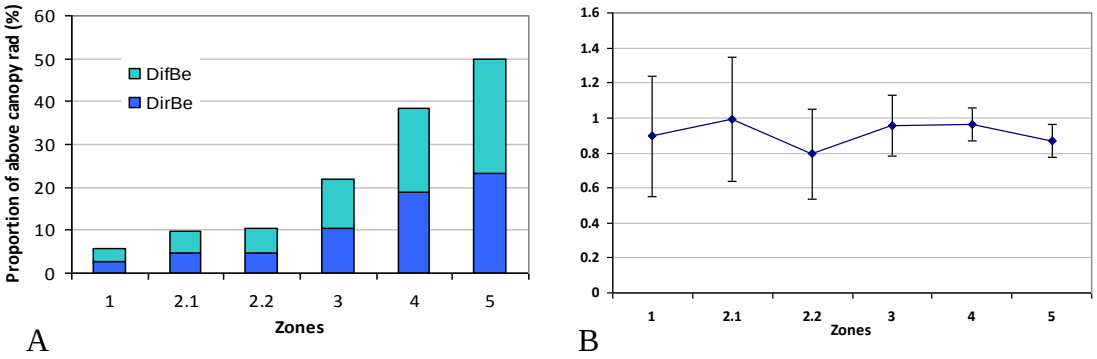


Fig. 14 A) Mean direct and diffuse fractions of radiation below the *Weinmannia* sp. crown as proportion of total above canopy radiation; B) variation in ratio of direct to diffuse below crown radiation among zones.

A study buddy – an Andean Spectacle Bear in a nearby *Ficus* sp. crown

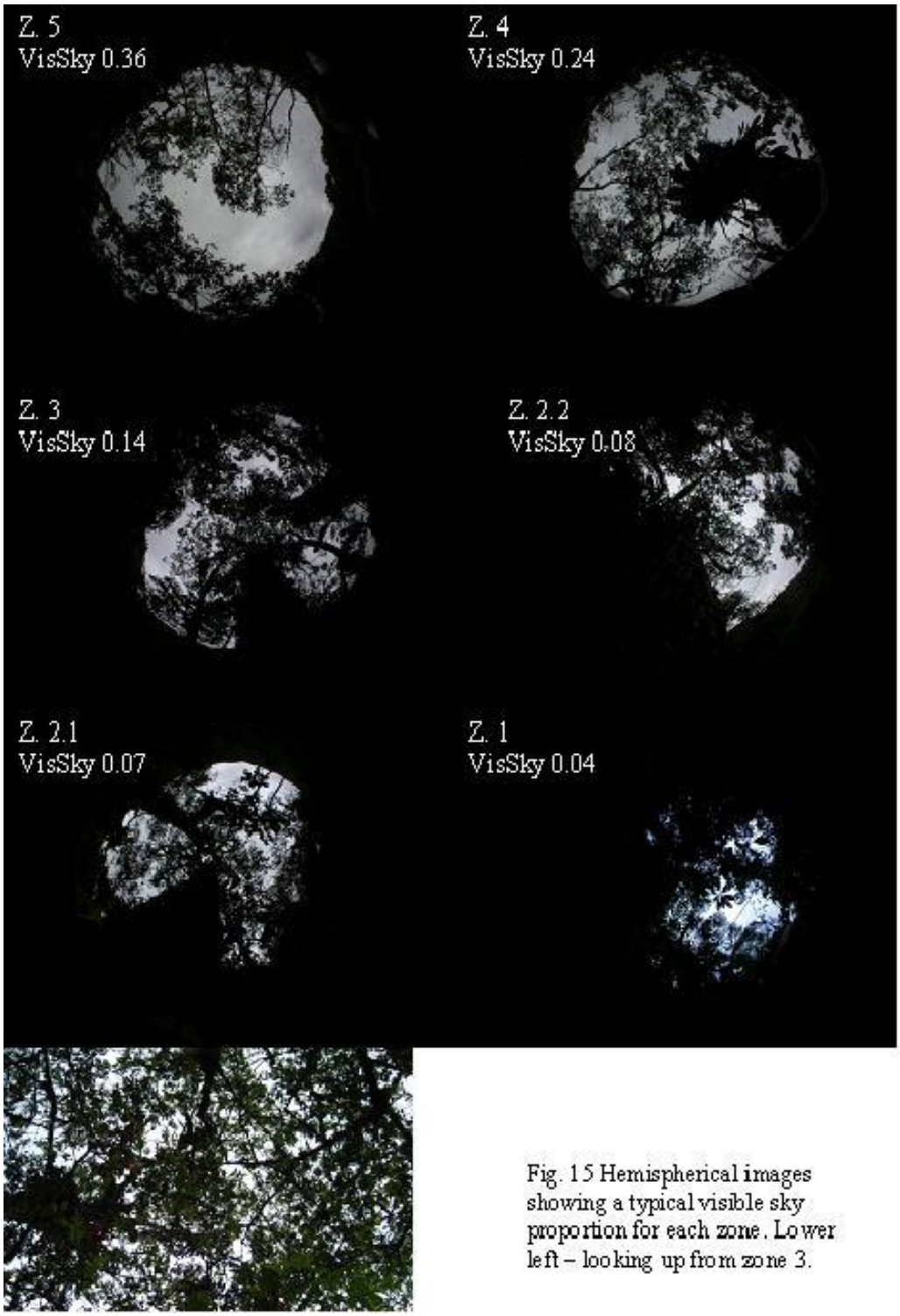


Fig. 15 Hemispherical images showing a typical visible sky proportion for each zone. Lower left – looking up from zone 3.

3.2.3 Associations

TotBe, DirBe and DifBe were all highly correlated (r > 0.97), as was VisSky with the radiation variables (r > 0.96) (Table 4). Temperature and RH were moderately negatively associated (r = -0.77). Temperature was moderately correlated with VisSky and the radiation variables (r = 0.75-0.79). LAI, temperature and VisSky were moderately negatively correlated (r = 0.77-0.88). RH and LAI were also moderately associated with each other and the radiation variables (r = 0.80-0.88).

Table 4. Associations between radiation related variables. All correlations (as Pearson's r) were significant at P < 0.001.

	RH	Temp	VisSky	LAI	TotBe	DirBe
Temp	-0.768					
VisSky	-0.803	0.751				
LAI	0.847	-0.774	-0.880			
TotBe	-0.811	0.787	0.984	-0.861		
DirBe	-0.801	0.789	0.959	-0.834	0.993	
DifBe	-0.810	0.775	0.995	-0.876	0.994	0.975

The results of the Kruskal-Wallis test for similarity among medians of zone temperature and RH values was significant (Temp, H = 763.15, 6, P < 0.001; RH, H = 181535.44, 6, P < 0.001). Similarity between medians among pairs of zones and above crown values was tested with Bonferroni adjusted Mann-Whitney test. Difference between all RH medians for zones and above the crown was found to be statistically significant (P < 0.0001). The test of temperature medians revealed a statistical similarity between zones 1 and 2.1, and zones 2.1, 2.2 and 3 (Table 5).

Table 5. Similarity between zone relative humidity (RH) medians, as identified by a Bonferroni adjusted Mann-Whitney test. RH medians in zones with the same letter was found to be statistically similar.

1	2.1	2.2	3	4	5	Above
A	A					
	B	B	B			

Observed differences between zone medians of radiation associated variables were found to be statistically significant.

VisSky	H = 54.03, 5, P < 0.001	TotBe	H = 53.64, 5, P < 0.001
LAI	H = 53.20, 5, P < 0.001	DirBe	H = 51.19, 5, P < 0.001
		DifBe	H = 53.81, 5, P < 0.001

Pairwise comparisons were also conducted using the Mann-Whitney test. The level of alpha was Bonferroni adjusted (Table 6).

Table 6. Statistical similarity of zone medians amongst the radiation associated variables revealed by Mann-Whitney pairwise comparisons. Medians in zones with the same letter were found to be statistically similar.

VisSky	**1**	**2.1**	**2.2**	**3**	**4**	**5**	**TotBe**	**1**	**2.1**	**2.2**	**3**	**4**	**5**
		A	A									A	A
LAI	**1**	**2.1**	**2.2**	**3**	**4**	**5**	**DirBe**	**1**	**2.1**	**2.2**	**3**	**4**	**5**
	A	A						A		A			
		B	B						B	B			
							DifBe	**1**	**2.1**	**2.2**	**3**	**4**	**5**
									A	A			

3.2.4 Diurnal fluctuation

Temperature

The overview provided by long term means of temperature and relative humidity in the crown reveal only part of the story about the microclimate in lowland rainforest canopies. Diurnal fluctuations add another important dimension that is essential to understanding the biogeography and tolerance characteristics of bryophyte species.

The lowest mean hourly temperatures and highest RH throughout the crown and above occurred near dawn, at 6 am. Zone 1 was the exception with its RH maxima (98.48%) at 10 am. The coolest place overnight and during early morning was zone 3 (Fig. 16). The temperature there dropped to 11.6˚C, 0.4˚C lower than above the crown at that time, which was also the warmest space during the night. Zones 4 and 5 were cooler, with 11.7˚C and 11.66˚C respectively. Zone 1 occupied had the middle rank of temperature at 6 am, with 11.81˚C. The mean temperature along the trunk was virtually the same as that above the crown, 12.01˚C in zone 2.2 and 12.03˚C in zone 2.1.

By 7 am, the below and above crown atmosphere begun its steady climb and maxima in all but zone 3 were reached at 3pm. Zone 3 peaked at 1 pm, but temperatures remained high between 1 and 3 pm throughout the profile. Between 7 and 9 am, the temperature gradient changed direction; the night cool mid and upper crown zones assumed their more expected position as the warmest in the profile.

At the warmest time of the day, zone 4 had the highest temperature (15.9˚C) closely followed by the crown periphery (15.87˚C). Zone 3 was a little cooler (15.6˚C), but warmer by 0.2˚C than the above crown air. Zone 1 and 2.2 shared a similar temperature of 14.9˚C, warmer than the bryophyte covered north-eastern side of the trunk, zone 2.1 with 14.8˚C.

The difference between coolest and warmest sections of the crown was greatest at 3 pm, but amounted to just 1.2˚C. The crown begun to cool from 4 pm. The temperature among zones and above the crown was most similar during the evening reversal of the temperature gradient around 7pm, when just 0.4˚C separated the above crown mean (warmest) and means for zones 2.1 and 2.2 (coolest). By 8 pm, the mid-crown, zone 3, already had the lowest temperature within the profile and by 2am, the bidirectional gradient in temperature described for 6am was already established. Ranges of temperature fluctuation within zones are presented in Fig. 17.

Relative humidity

The decreasing gradient of RH from the ground to the tree top was well defined even at night (7.8% difference) (Fig. 16). At 6 am, zone 1 was most humid (98.3%), but interestingly, zone 4 was a little less saturated (93.26%) than the more distant from the ground zone 5 (93.67%). Zones 2.1 and 2.2 had the same RH (95.8 %), while the mid-crown, zone 3, averaged 94.3%. The air above the crown also reached its most saturated at this time (90.5%).

In the morning, as temperature rose, RH begun to fall and the difference between the upper crown zones and above crown RH quickly diminished. By 10 am all three shared a similar level of saturation. While the upper profile converged, zones 2.1 and 2.2 along the trunk begun to separate, with the RH of the less epiphyte rich 2.2 rising faster than 2.1.

The lowest hourly mean RH was recorded between 1 and 3 pm. Zone RH generally had a negative relationship with height above the ground. At 3 pm, zone 1 reached its lowest hourly mean level of saturation (97.52%), just 0.96% lower than its maximum at 6 am. The difference between zone 1 RH and the above canopy mean at that time rose to 14%. Zone 2.1 had the second highest RH (92%) and was more saturated than zone 2.2 (90.9%) on the more exposed side of the trunk. Zone 3 RH (87%) was more similar to that of the upper crown and above crown levels than mean values recorded for the trunk. Zone 4 RH was 84.4%, just 0.6% more than the mean for zone 5 (83.8%). Only 0.3% separated zone 5 (83.8%) from the above crown mean (83.5%). From 4 pm, RH begun to climb while temperature dropped. By 5 pm, means for zone 5 indicated more saturated conditions there than in zone 4, as observed during the night and early morning.

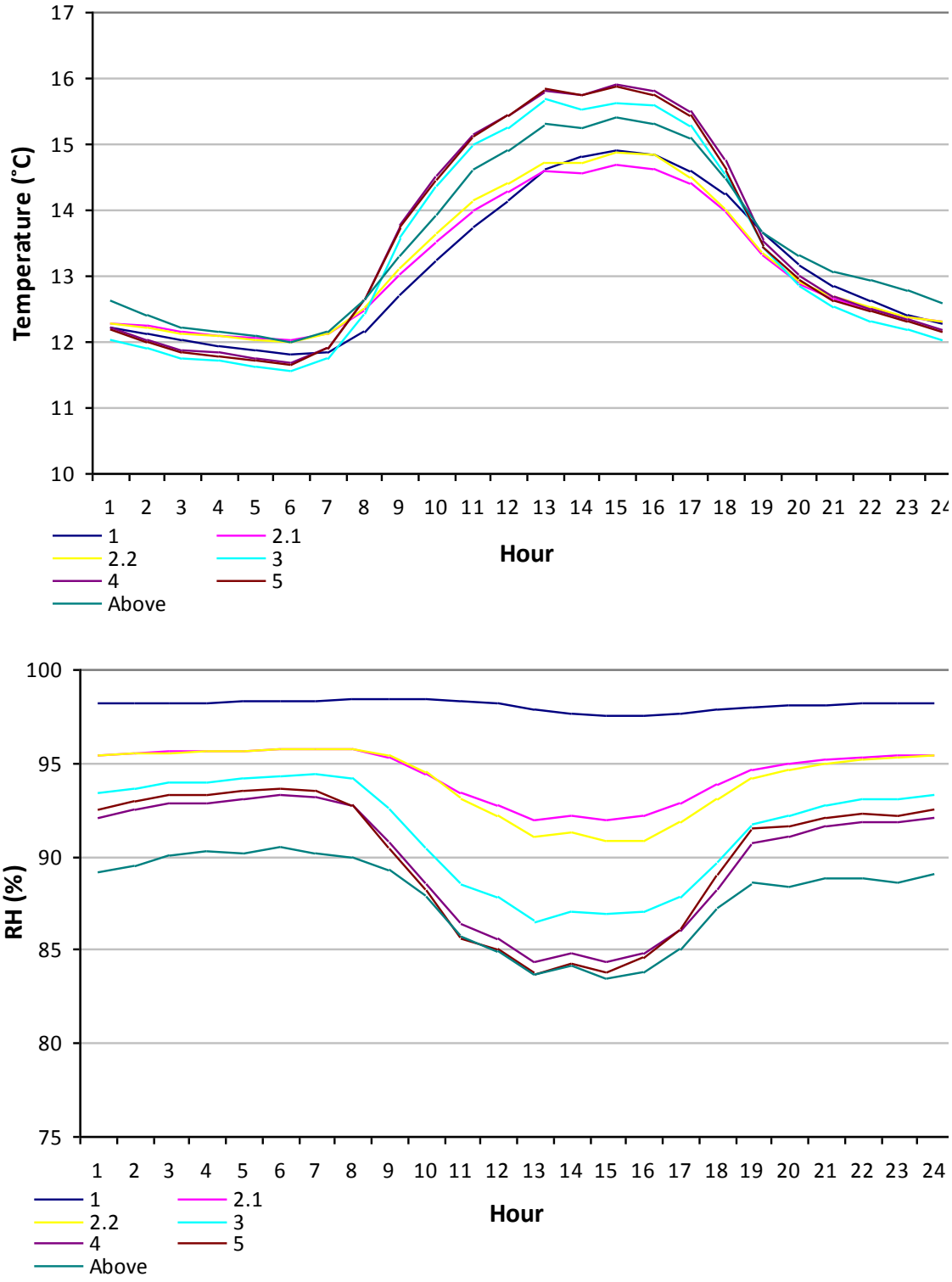


Fig. 16 Hourly mean temperature and relative humidity in Johansson zones and above the crown, over the study period.

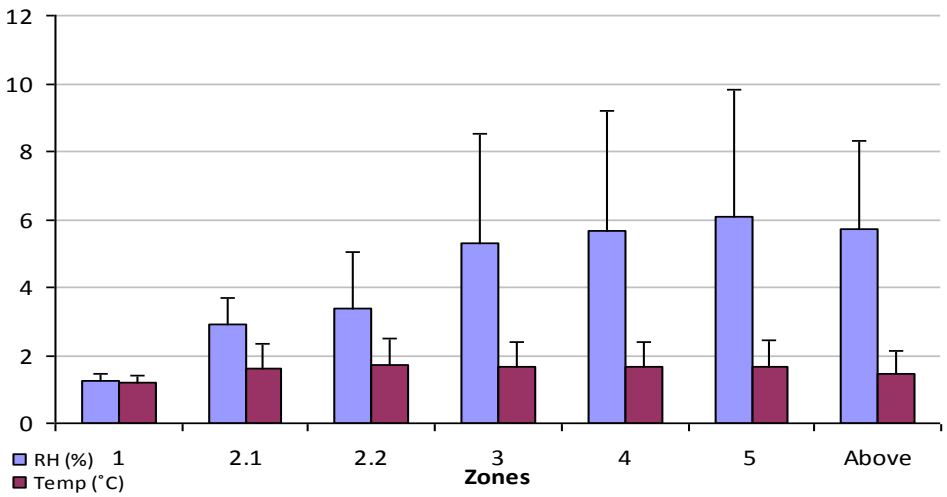


Fig. 17 Means of interquartile ranges for hourly relative humidity and temperature in Johansson zones and above the canopy.

Different weather conditions

The tendencies presented above are averages that smooth over the influence of different weather conditions. A sample of hourly temperature and RH fluctuations on a rainy and dry, sunny day are presented in Appendix II. Analysis of the influence by various climatic conditions on the average diurnal pattern of RH and temperature fluctuation is beyond the scope of this study, but it is clear that the different frequencies of each type of weather within a study period have the potential to change the average pattern presented here. October 2006 was a little warmer and wetter than average, while November was cooler and recorded 51% more rain than average for that month (Table 7). The interquartile range of RH and temperature fluctuation within zones, as recorded in the present study, is presented in Fig. 17.

Table 7. Means for temperature, relative humidity, photosynthetically active radiation and precipitation for October and November (Catchpole, D. 2007, pers. comm.) and values for the same period in 2006.

	Temp (˚C)	RH (%)	PAR	Rain (mm)
Oct mean	13.87	92.3	289.9298	208.16
Oct-06	14.28	88.9	268.099	232.66
Nov mean	14.18	93	284.685	212.66
Nov-06	13.49	89	266.087	321.31

3.3 Discussion

3.3.1 Habitat stability near the ground

Each of the monitored climate and radiation associated parameters displayed a different pattern of data range. A rich mosaic of microclimates exists along the altitudinal gradient from the ground to above the canopy, but generally, stability of microhabitat climate within the host decreased with distance from the ground.

The exceptional stability of climate near the ground in rainforests has also been observed elsewhere (Kira and Yoda, 1989; Freiberg, 1997). The observed mean daily range in temperature of 3.1˚C is comparable to the 3.5˚C range found in a Pasoh rainforest, Malasia by Aoki *et al*. (1975). The RH near the ground in Pasoh also remained high, 96-100%. The mean hourly RH in zone 1 at the El Cedro site did not fall below 97.5% and had an average diurnal range of just 0.96%.

Based on lowland rainforest studies, Kira and Yoda (1989) report very high radiation interception rates for rainforest canopies. An average of just 0.4% of above canopy PAR reached the forest floor in Pasoh (Aoki *et al*. 1975). Zone 1 of the *Weinmannia* received an average of 5.9% of above crown PAR, highlighting the difference between the structures of closed lowland rainforest canopies and the broken canopies that are more

characteristic of steep montane sites. The LAI for trees in a lowland montane forest in Puerto Rico investigated by Odum *et al.* (1970) was 6.3, much higher than the average of 3.5 recorded below the open crown of the *Weinmannia*. The greater presence of bryophytes at ground level in montane forests is explained by Gradstein *et al.* (2001) with higher presence of organic material, more quickly decomposed in warmer lowland environments. Higher PAR availability on the floor of the more heterogeneous montane forests may also contribute to this variation in species density.

3.3.2 The two faces of the trunk

The trunk zones 2.1 and 2.2 experienced even less extremes fluctuations of temperature, but varied more over a 24 hour period. The lower overall temperature range along the trunk may reflect its simpler structure, lacking the variety of microsites afforded by buttressing in the lower section of zone 1.

Mean VisSky value for zone 2.2 was just 1.4% greater than the mean recorded for zone 2.1 and medians for both zones were found to be statistically similar, yet the former supported an obviously less dense population of epiphytic bryophytes. The diffuse fraction of the total below radiation was 20% higher in zone 2.2 than on the sheltered side of the trunk; the TotBe was just 7% higher. Both sites shared a similar temperature and RH at night, but it is the day time fluctuations that most separate these two microhabitats. Zone 2.2 warmed up more quickly and on average maintained higher temperature longer than zone 2.1. Elevated temperature had an opposing effect on RH, making zone 2.2 both drier and warmer.

3.3.3 Impact of crown architecture and epiphytes on microclimate

Zone 3 was the coolest place to spend the night in the *Weinmannia* host. This agrees with the findings of Freiberg (1997) and Aoki *et al.* (1975). Both report lowest night time temperatures in the mid-crown and highest day time temperatures near the crown periphery. Freiberg (1997, 2001) found that a thick cover of epiphytes, predominantly moisture storing bryophytes, depressed temperature and maintained high RH around branches. An opposing trend is reported by Zotz and Thomas (1999). They recorded

higher mean day time temperatures for branch surfaces in *Annona* sp. crowns than above canopy air, despite being partially shaded by the crown foliage. Zones 3, 4 and 5 recorded higher temperature during the day than the air above the crown, but contrary to the general negative relationship between temperature and RH, maintained higher levels of RH. Evaporation from the epiphytic bryophyte mats may have contributed to the observed elevated levels of RH. Low interception of radiation by the sparse *Weinmannia* crown may encourage heating of branches and depletion of the stored moisture, masking the night temperature moderating influence of epiphytes found by Freiberg (2001) in his study conducted in a wetter environment in French Guiana. Epiphytic bryophytes may rely heavily on the frequent nightly low cloud to replenish their store of moisture, particularly during the dry season.

The opposing gradient of increasing temperature and dropping RH with height above the ground was interrupted by a reversed trend between zones 4 and 5. The outer crown receives more radiation, has lower LAI and should be warmer than the less irradiated zone 4. This slight, but significant bump in the gradient could be explained by the *Weinmannia*'s crown architecture and net diurnal fluctuations of both RH and Temperature in the two zones.

The majority of the feathery foliage of the *Weinmannia* was concentrated in open heads near the tips of branches (Fig. 17). Better ventilation at the crown periphery, evapotranspiration and lower biomass of the twiggy crown could contribute to the slightly lower hourly average temperature recorded for zone 5 during the warmest part of the day than the mean for the more sheltered and biomass richer zone 4. In the evening, lower temperature in zone 5 could reflect a more rapid loss of heat from the outer crown (Szarzynski and Anhuf, 2001), contributed by higher ventilation and lower biomass volume[5]. At night, the temperature in both zones is similar, but the humidity is on average 0.4% higher in zone 5 than zone 4 in the 10 hours between 10 pm and 6 am. The study site is frequently bathed in fog during the nigh and early morning. Chang *et al.* (2006)

[5] The value of biomass for amelioration of temperature fluctuations is demonstrated by the slower rate of cooling displayed by the trunk (zones 2.1 and 2.2) during the night (Fig. 16)

showed that 50% of the fog capture by crowns occurred in the outer crown. Condensation of fog on the foliage, predominantly located in the outer crown, may explain the higher mean night RH in zone 5, despite a similar temperature to zone 4.

The influence of crown architecture and epiphyte presence on crown microclimate is illustrated by the contrasting findings of this study and the proximately conducted study by Catchpole (2004). The leaf type and crown architecture of the *Ficus crassiuscula* in the Catchpole study was starkly different to the *Weinmannia* sp. host used in this study. The *Ficus* had a dense (VisSky in zone 3 = 5%), heavier and more horizontally branched crown particularly rich in vascular epiphytes including a high proportion of bromeliads. In contrast, the *Weinmannia* had a fine architecture of predominantly upright branches forming an open crown (VisSky in zone 3 = 14.6%), was rich in predominantly epiphytic bryophytes, and did not have a large accumulation of organic soil. High population of bromeliads was found by Zotz and Thomas (1999) to depress mean temperature of host branches. The high bulk density of vascular epiphytes and high water storage capacity, particularly common among the Bromeliaceae (Benzing, 1998), could ameliorate temperature fluctuations in crowns and together with greater radiation interception by some canopy species produce vastly contrasting pictures of crown microclimate in lower montane rainforests.

3.4 Conclusion

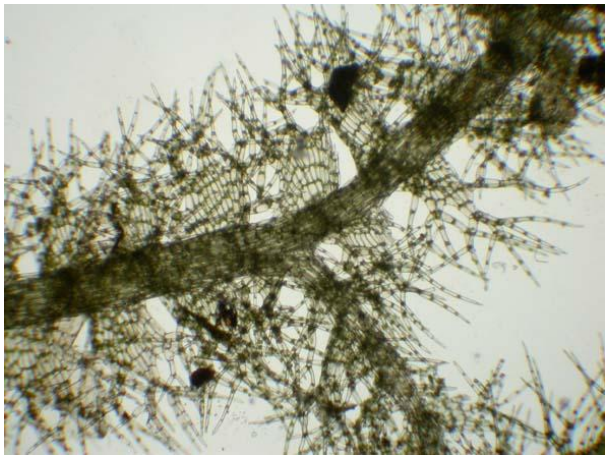
The microclimate patterns existing in the *Weinmannia* sp. growing in at the upper margin of the lower montane belt largely agree with findings of studies conducted in rainforests at lower elevations (Freiberg, 1997; Szarzynski and Anhuf, 2001).

An opposing gradient of temperature and relative humidity existed from the ground to above the canopy. During daylight, the gradient is influenced by solar radiation, progressively intercepted with distance from the crown periphery and reflected by increasing LAI and decreasing proportion of visible sky. Fluctuations within sections of the crown are influenced by the presence of water storing epiphytes, largely consisting of

bryophytes. The density stratification of the heated air in the upper part of the canopy and the denser cool air in the understorey observed in lowland rainforest was not as pronounced as indicated in literature (Szarzynski and Anhuf, 2001). Mean LAI near the ground (3.5) was lower and the visible proportion higher than means reported for trees in lowland rainforest (Aoki *et al.*, 1975; Kira and Yoda, 1989). There appeared to be adequate penetration of radiation throughout the crown, resulting in a smaller difference (just 1.2˚C) in average values between the coolest (lower trunk) and warmest (outer crown) parts of the tree at the warmest time of the day (3 pm), than reported for forests at lower elevations (Freiberg, 1997; Szarzynski and Anhuf, 2001). The gradient in RH was steeper; 13.72% separated the lower trunk and the crown periphery, 14% to the above canopy mean for 3 pm.

After sunset, rapid radiative cooling of the outer crown induced a reversal of the temperature gradient. Coolest temperatures at 6 am were recorded at the mid-crown, while the above crown temperature was higher than any section of the tree. This is similar to patterns found in rainforests at lower altitudes, and agrees the nocturnal decoupling of the crown from the atmosphere observed by Szarzynski and Anhuf (2001) in lowland Venezuela. Variability of the crown microclimate appears to increase with height above the ground.

The contrasting findings of a study (Catchpole, 2004) conducted in close proximity to this project, highlight the heterogeneity of lower montane rainforest habitats and encourage further studies to be undertaken in this poorly explored environment.



***Trichocolea flaccida*, a lower trunk faithful species.**

Chapter 4. Epiphytic bryophytes on *Weinmannia* sp.

4.1 Background

Most studies of bryophyte ecology tend to be conducted over large areas and very few single tree studies are reported in literature. Iwatsuki and Hattori reported 78 species on a mature *Abies firma* and 58 species on a *Tsuga sieboldii* growing at 700 m in Wari'iwa Valley (1956a) and 47 species on a mature *Cryptomeria japonica* at 650 m on the slopes of Mt. Ichifusa, Japan (1956b). A survey of a Tasmania endemic conifer, a fallen mature *Lagarostobos franklinii* (Huon Pine) in western Tasmania found 55 bryophyte species (Jarman and Kantvilas, 1995a). Other surveys in cool temperate montane forest of western Tasmania revealed 54 and 48 species growing on another endemic conifer, *Athrotaxis selaginiodes* (King William Pine) and a *Nothofagus cunninghamii* (Myrtle Beech) respectively (Romanski, 2005 unpublished). Milne and Louwhoff (1999) found just 26 species on a *N. cunninghamii* growing in a drier environment of central highlands, Victoria, Australia. The range of habitats, age, size and species of the surveyed hosts makes any meaningful comparison of diversity supported by a single host difficult, although all of the above studies demonstrate the importance of trees as substrate for bryophytes.

Bryophytes have a greater tolerance to a range in temperature than vascular species, but are more sensitive to fluctuations in moisture levels (Lee and La Roi, 1979). The variation in ratio of epiphytic mosses to liverworts between habitats has also been attributed to the variation in the availability of moisture (Barkman, 1958; Wolf, 1993a; Jarman and Kantvilas, 1995b). Mosses tend to dominate under xeric conditions, while hepatics flourish with greater availability of moisture. Jarman and Kantvilas demonstrated that this pattern extends to relatively wet environments by examining the ratio of mosses to hepatics in progressively wetter cool temperate rainforest formations in Tasmania (1995b). On a finer scale, hepatics often heavily outnumber mosses in the generally more mesic environment of the lower trunk, while in the canopy, this ratio becomes more equitable (Wolf, 1995; Kürschner and Parolly, 1998). Plasticity in community composition and succession influenced by moisture availability has been reported by Peck *et al.* (1995).

Mesic conditions were found to encourage early establishment of late-successional species and extend the distribution of facultative epiphytes to higher levels on tree hosts.

The majority of bryophytes species in rainforest are epiphytes and this characteristic has been exploited by various ecologists to capture a large proportion of the total bryophyte diversity simply by collecting corticolous species (Gradstein *et al.*, 1994; Gradstein, 1995; Sillett *et al.*, 1995; Gradstein *et al.*, 1996; Kürschner and Parolly, 1998). The aim of the present study was to provide a glimpse of the bryophyte diversity in lower montane rainforest of the Peruvian Yungas by sampling a single, canopy co-dominant, *Weinmania* sp. host.

4.2 Results

Methods are presented in Chapter 2, section 2.4.

4.2.1 Floristics

One hundred and ten species of bryophytes (77 liverworts, 1 hornwort and 32 mosses) were found on the *Weinmannia* host (Table 8). The hepatic collection included 41 genera in 15 families, while 23 genera in 17 families were recorded for mosses (Appendix III). The most genus rich moss families were Meteoriaceae (3), Pilotrichaceae (2) and Pottiaceae (2). Among the hepatics, Lejeuneaceae was by far the most diverse family with 23 genera. In second place were Aneuraceae, Geocalycaceae, and Jubulaceae with just two genera each. At species level, *Lejeunea* and *Frullania* provided six species each, while the most species rich genera among the mosses were *Zygodon* (4) and *Marcomitrium* (3) (Table 9). The hepatics included just one hornwort species, *Dendroceros crispus*.

Table 9. Genera with highest number of species on the *Weinmannia* host.

Mosses		Hepatics	
Zygodon	4	*Lejeunea*	6
Macromitrium	3	*Frullania*	6
Meteoridium	2	*Lophocolea*	4
Trachyxiphium	2	*Drepanolejeunea*	4
Porotrichum	2	*Leptoscyphus*	2

Table 8. The proportion of subsamples in which taxa were present in each zone of a single *Weinmannia* sp. host, lower montane rainforest, Peru.

	Zone					
Species	**5**	**4**	**3**	**2.2**	**2.1**	**1**
Drepanolejeunea araucariae var. *araucariae*	0.1					
Lejeunea subgen. *Lejeunea* sp. 3	0.1					
Anopolejeunea conferta	0.2					
Lejeuneacea sp. 2	**0.8**					
Frullania stenostipa *	**0.7**					
Frullania sp. 5	0.4					
Diplasiolejeunea sp.	0.4					
Aureolejeunea fluva *	0.3					
Colura tenuicornis	0.1					
Chielolejeunea subgen. *Strepsilejeunea* sp. 2	0.3					
Brachiolejeunea spruceana *	**0.8**	0.1				
Amphilejeunea reflexistipula *	0.1	0.1				
Mnioloma cyclostipa		0.1				
Squamidium leucotrichum		0.1				
Brachymenium consimile		0.1				
Macromitrium longifolium		0.1				
Macromitrium podocarpi		0.3				
Leptoscyphus physocalyx		0.2				
Leptoscyphus porphyrius		0.3	0.5			
Squamidium livens		0.4	0.1			
Plagiochila sp. 5		0.4	0.3			
Streptopogon calymperes		0.1	0.1			
Plagiochila sp. 2		0.4	0.2			
Lejeunea sp. 3		0.2	0.2			
Aneura pinguis		0.1	0.2			
Oryzolejeunea sp. (ad aff *O. venezuelana*) *	0.5	**0.7**	0.3			
Frullania subgen. *Frullania* sp. 1	0.1	0.1	0.1			
Dendroceros crispus	0.1	0.1	0.2			
Microlejeunea colombiana	0.5		0.1			
Frullania apiculata *	0.3		0.1			
Meteorium illecebrum		0.2	0.1			
Lophocolea trapezoidea			0.1			
Syrrhopodon graminicola *			0.1			
Ceratolejeunea maritima *			0.3			
Plagiochila sp. 4			0.2			
Trachyxiphium variable			0.1			
Macrolejeunea pallescens fo. *lancifolia*	**0.7**				0.1	
Odontolejeunea lunulata	0.1				0.1	
Macromitrium aureum		**0.9**	**0.7**		0.2	
Neurolejeunea breutelii *		0.5	**0.9**	0.1	0.3	
Plagiochila sp. 3		0.3	0.6	0.1	0.5	
Riccardia metzgeriaeformis		0.2	0.1		0.1	
Papillaria imponderosa		0.2	0.5		0.1	
Trichocholea filicaulis *		0.1	0.3		0.1	
Zygodon reinwardtii	0.1	0.4	0.5	0.4	0.5	
Harpalejeunea sp.	**1**	0.2	0.5		0.6	
Frullania brasiliensis *	**0.9**	**1**	**0.9**		0.5	
Lepidolejeunea eluta	0.1	0.5	**0.7**	0.1	0.5	
Drepanolejeunea infundibulata *	**0.8**	**0.7**	0.6	0.1	0.2	
Plagiochila sp. 1	0.1	0.2	0.4	0.4	0.3	
Cheilolejeunea comans *	0.5	**1**	**0.7**	0.1	0.6	
Frullanoides densifolia subsp. *densifolia*	**0.8**	**1**	**1**	0.1	0.3	
Frullania riojaneirensis	**1**	0.4	0.3		0.1	
Ceratolejeunea deciscens *	0.3					0.1
Lejeunea subgen. *Lejeunea* sp. *2*	0.2		0.6	0.5	**0.8**	0.1
Omphalanthus filiformis	**0.8**	**0.9**	**1**	0.5	**0.7**	0.1
Lejeunea subgen. *Lejeunea* sp. 1	0.2	0.7	0.2	0.1	0.2	0.3
Daltonia longifolia	0.3	0.1	0.1		0.1	0.1
Plagiochila bifaria	0.2	**0.8**	0.6		0.1	0.1
Lejeunea subgen. *Nanolejeunea* sp.	0.1	0.1	0.4	0.1	0.5	**1**
Metzgeria decipiens	0.1	0.2	0.4		**0.7**	**0.7**
Macrolejeunea pallescens	0.2	**0.8**	**0.7**	**0.8**	**1**	**1**
Prionodon densus		0.3	0.5	**0.8**	**0.8**	0.1
Meteorium remotifolium		0.2	0.7	0.3	**0.8**	0.1
Mittenothamnium reptans		0.1	0.1	0.2	0.5	0.3
Radula montana		**0.8**	**0.7**	0.1	**0.8**	**1**
Taxilejeunea pterigonia		0.2	**0.8**	0.1	**0.7**	0.4
Plagiochila stricta		0.1	**0.7**	0.5	1	**0.8**
Dicranolejeunea axillaris *		0.1	0.3	0.4	0.6	0.3
Lepidopilum caviusculum *		0.1		0.1	0.2	0.5
Porotrichum longirostre		0.4	**0.7**	0.4	1	1
Lejeuneacea Tribe *Lejeuneae* sp. 1		0.1	0.1	0.4	**0.7**	0.6
Brachiolejeunea leiboldiana *		0.1				0.1
Leiomela bartramioides			0.1		0.5	0.3
Zygodon gracilliums *			0.1	0.4	0.1	
Zygodon obtusifolius			0.1	0.2	0.1	
Trichostomum brachydontium			0.3	0.1	0.2	
Lepidopilum scabrisetum			0.1		0.1	
Acrobolbus antillanus			0.1		0.1	
Lepidolejeunea spongia			0.1		0.1	
Plagiochila sp. 6			0.1		0.1	
Porotrichum substriatum			0.1	0.1		0.2
Trachyxiphium subfalcatum			0.1			0.2
Pallavicinia lyellii			0.1			0.4
Lophocolea sp.			0.1			**0.7**
Lejeunea sp. 2			0.1			0.2
Lophocolea coadunata			0.1			**0.8**
Plagiochila sp. 7				0.1	0.1	0.2
Thuidium peruvianum				0.1	0.4	0.1
Sematophyllum galipense				0.1	0.1	
Plagiochila sp. 9					0.1	
Cephaloziella granatensis					0.1	
Leptolejeunea elliptica					0.2	
Plagiomnium rhynchophorum					0.2	0.6
Hypopterigium tamarisci					0.4	0.6
Metzgeria leptoneura					0.2	0.2
Prionolejeunea equitexta *					0.1	0.2
Prionolejeunea decora *					0.4	0.4
Plagiochila aerea *					0.1	0.1
Fissidens serratus						0.2
Plagiochila sp. 8						0.2
Jubula pensylvanica subsp. *bogotensis* *						0.4
Riccardia smaragdina *						0.6
Rhizogonium novae-hollandiae						0.5
Monoclea gottschei						0.1
Lepidozia caespitosa						0.1
Holomitrium arboreum						0.1
Lophocolea muricata						0.4
Trichocholea flaccida						0.2
Plagiochila harrisana						0.3
110 species Zone totals:	37	52	64	30	55	46

* - not previously recorded for Peru

Species composition and abundance at each zone varied (Table 8, Fig. 18). The most species rich sections were the mid-crown, zone 3 (64 spp.) and the sheltered side of the trunk, zone 2.1 (55 spp.) Not surprisingly, least epiphytes were found along the exposed side of the trunk, zone 2.2 (just 30 spp.). The outer crown, zone 5, supported a surprising diversity of bryophytes (37 spp.). Distribution of the species suggests the presence of specialists with narrow habitat preferences and more widely occurring generalist species.

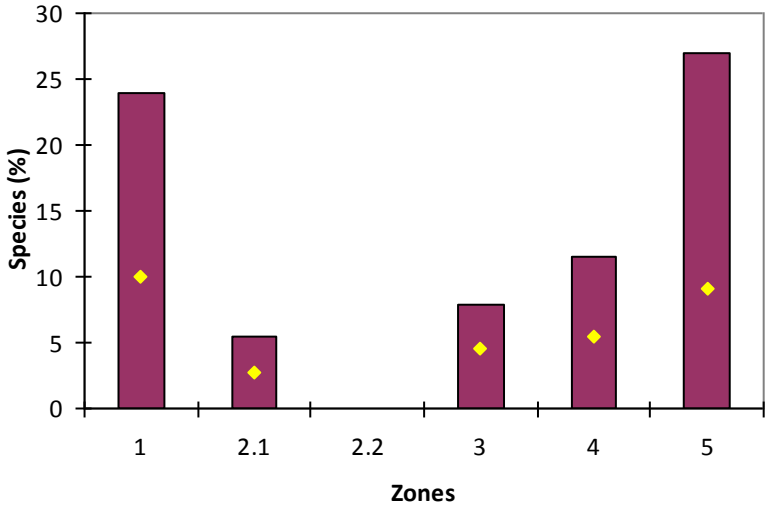


Fig. 18 Proportion of species confined to each zone and the proportion that zone exclusive species contributed to the total number of bryophytes found on the Weinmannia host (inset marker).

Just one moss, *Daltonia longifolia*, was found with low frequency throughout the host, except on the dryer side of the trunk. All others were found over a more restricted microhabitat range. Among the hepatics, the generalists were *Omphalanthus filiformis*, *Macrolejeunea pallescens* and some members of the Lejeuneaceae. *Plagiochila bifaria* had a similar distribution to the *D. longifolia* and was not recorded in zone 2.2.

Overall, hepatics outnumbered mosses by 2.44:1, but this ratio also varied considerably between zones (Fig. 19). Just 2 moss species were found in the outer crown, making up less than 6% of the entire zone 5 species richness. Appressed, weft and pendant forms of the Lejeuneaceae and Jubulaceae outnumbered mosses by 17.5:1. The lowest hepatic to moss ratio was recorded for the exposed side of the trunk (1.5).

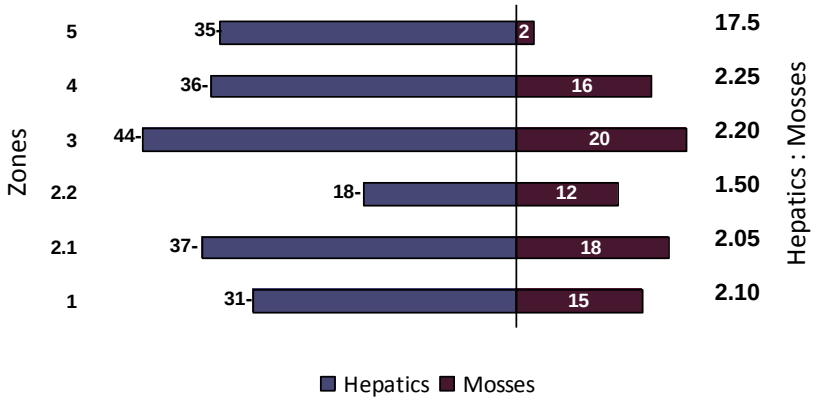


Fig. 19 Hepatic and moss species and the ratio of hepatics to mosses (right) in Johansson zones.

Based on available literature about habitat preferences of each species (Gradstein et al., 2001; Appendix I), obligate epiphytes made up 31% of the *Weinmannia*'s species richness. A larger proportion of mosses (35%) than hepatics (29.5%) were obligate species, although this fraction in both groups rose sharply in the outer crown. An increase in the proportion of obligate mosses was also detected in the drier and warmer zone 2.2 (Fig. 20).

Broadly distributed species made up the largest proportion (46%) of the epiphytic community on the *Weinmannia*. These generalists were also frequently the most common species in each zone (Table 8). Twenty one percent of the species were confined to the trunk, while 33% were only found in the crown.

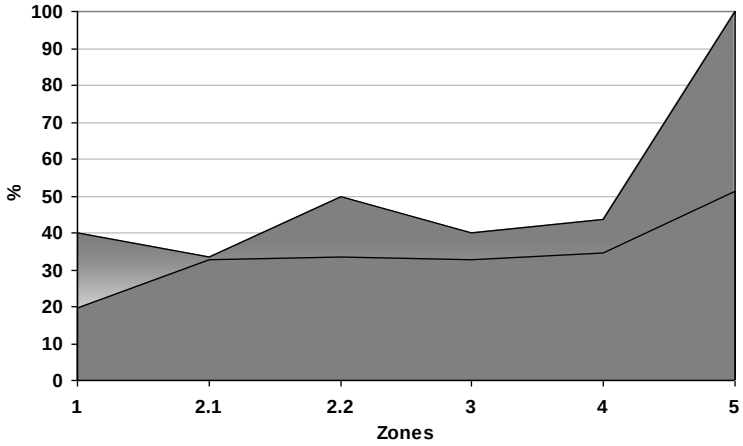


Fig. 20 The proportion of obligate mosses (light grey) and hepatics (dark grey) in each zone.

The wet base

The lower trunk presented a heterogeneous microhabitat of buttresses and deeply shaded folds (Fig. 21). It supported 42% of the total species richness recorded for the *Weinmannia* host; 22% of those were only found on the shady trunk base. Among the lower trunk specialists were the hepatics *Riccardia smaragdina*, *Lophocolea muricata*, *Jubula pensylvanica* and *Plagiochila harrisana*. *Radula montana* was common.

The featherform *Rhizogonium novae-hollandiae* and tiny *Fissidens serratus* together with the dendriform *Hypopterigium tamrisci* were among the moisture loving mosses found with high frequency on the lower trunk and extending into zone 2.1 respectively. The robust pendulous moss *Porotrichum*

Fig. 21 The south-western, more exposed side of the lower trunk. The white line crossing the image is part of a grid delimiting subsections of a 1 ha study plot used in complementary studies.

longirostre was quite common throughout the moister sections of the host, and was recorded as high as zone 4. The bryophytes did not densely cover the trunk, but formed a sparse mat of weft growth-forms framed by *P. longirostre*

Sheltered side of the trunk

Many of the bryophytes in zone 2.1 (Fig. 22) were species with broad distributions throughout the host. Some canopy species like *Drepanolejeunea infundibulata* and *Frullania* species also descended to this level. *Plagiochila stricta* was most frequently found here, as were hepatics *Dicranolejeunea axillaris* and some *Lejeunea* species, and the mosses *Mittenothamnium reptans*, *Leiomela bartramioides* and *Meteorium remolifolium*. The sheltered side of the trunk had just three unique species, all hepatics, *Leptolejeunea elliptica*, *Cephaloziella gratanensis* and *Plagiochla* sp. 9.

Fig. 22 Site 2.9. Thick species rich mats were typical along the sheltered side of the trunk. Note the presence of lianas and vascular epiphyte roots adding complexity to the otherwise smooth trunk.

Exposed side of the trunk

In contrast, large sections of the southwestern side of the trunk were dominated by crustose lichens and were bare of bryophytes (Fig. 23). No zone limited species were found in zone 2.2. The bryophytes growing here were a much reduced and less abundant selection of species found on

Fig. 23 Site 2.10, at the same height but opposite side of the trunk to the above pictured site 2.9. The moss, being encroached upon by foliose lichens, is *Prionodon densus*.

the sheltered side of the trunk. The most common species was *Prionodon densus*, and the omnipresent *Omphalanthus filiformis*, closely followed by *Plagiochila stricta*. Surprisingly, *Macrolejeunea pallescens* and a host of other seemingly fragile Lejeuneaceae were also found here. Mosses represented 40% of the assemblage in this zone, a proportion greater than found on any other part of the host.

The large branch bases

The carpet of epiphytic bryophytes was up to 50 mm thick on the bases of the canopy scaffold branches. The interwoven, multi strata community provided enough organic matter for growth of terrestrial pteridophytes and germination niches for vascular epiphytes (Fig. 24). A large proportion of the species had broad distributions in the *Weinmannia*, similarly to zone 2.1. The zone also included extensions of upper crown and trunk species distributions, making it the most species-rich section of the host. The widely distributed *Frullania densifolia* and *O. filiformis* reached their highest frequency in zone 3, as did *Neurolejeunea brutelii*, *Lepidolejeunea eluta* and *Taxilejeunea pterigonia*. Apart of the common *P. longirostre*, the more frequent mosses included *Meteorium remotifolium*, *P. densus* and *Zygodon reinwardtii*, but even those were generally found less frequently than most of the hepatics. Two of five species only found in zone 3 were mosses *Trachyxiphium variable* and *Syrrhopodon graminicola*.

Fig. 24 The high-rise of bryophytes - base of the eastern leader. Sixty four species were found in zone 3 and a mean of 22.2 species were recovered from 0.03 m^2 samples.

Mid-outer crown

The middle third of the branches remained well covered with bryophytes, but also included more foliose lichens than was found lower in zone 3. *Cheilolejeunea comans*, *Plagiochila bifaria* and the moss *Macromitrium aureum* were recovered most frequently in zone 4. The broadly distributed *Frullania brasiliensis* also reached its peak frequency here. Six species were only found along the branches of this section, four of them mosses: *Macromitrium podocarpi*, *M. longifolium*, typical canopy species, *Brachymenuim consimile* and *Squamidium leucotrichum*. The rare hepatics were *Leptoscyphus physocalyx* and *Mnioloma cyclostipa*.

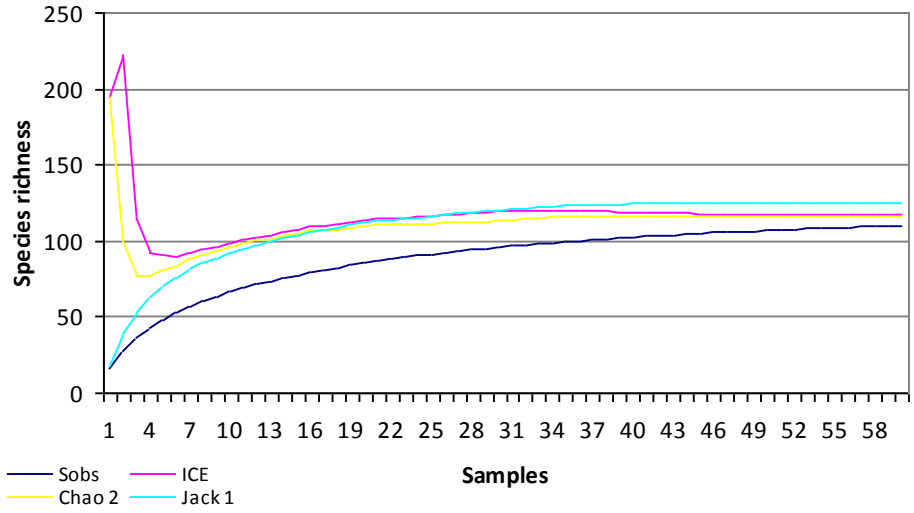
Fig. 25 The *Weinmannia* had an open, twiggy crown. Looking up the exposed side of the trunk

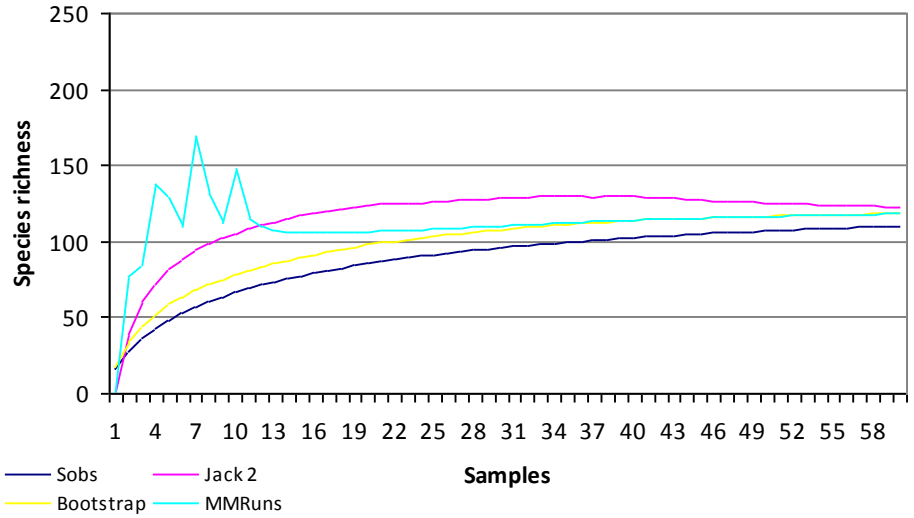
The outer crown

The hepatics dominate the outer crown (Fig. 25 & 26). Seventeen times more hepatic species than mosses were found in this most variable of microhabitats on the *Weinmannia*. The only other niche competitors are lichens, predominantly the abundant fruticose species. This zone also recorded the highest proportion of faithful species; 27% of the zone community and 9% of the entire tree epiphytic population of bryophytes (Fig. 26).

Fig. 26 *Frullania riojaneirensis* doing battle with fruticose lichens for supremacy of the twig kingdom.

The outer crown specialists included *Frullania stenostipa* and the handsome *Colura tenuicornis*, among other *Frullania* and Lejeuneaceae species (Table 8). *Brachiolejeunea spruceana*, *Frullania riojaneirensis* and the slender form *lancifolia* of *Macrolejeunea pallescens* had their highest frequency in zone 5, as did the obligate moss *D. longifolia*.





Chao 2	115.74
ICE	118.03
Bootstrap	118.46
MMRuns	118.21
Jack 2	123.10
Jack 1	124.75

Fig. 27 Species accumulation curve of the observed species (Sobs) on the *Weinmannia* host and predictions of species richness by some of the popular estimators.

4.2.2 Species capture and richness estimation

The single host study using 60 subsamples recorded 992 species counts. Fifteen species were found just once and additional 17 were found just two times on the *Weinmannia* host. The Fisher's alpha diversity index for the single host was 31.64 and the Simpson (inverse) index, 53.2.

The mean estimate of species richness provided by six estimators is 120 species (Fig. 26), just 9% above the number observed. Confidence in the estimates is added by the leveling off of plotted Fisher's alpha and the Simpson indexes, despite a continuing slope at the right hand end of the species accumulation curve (Fig. 28). The study appears to have adequately captured the *Weinmannia'*s epiphytic bryophyte diversity. Interestingly, both the Chao2 and ICE on average provided 49% and 44% respectively higher estimates for likely species diversity at the zone level (Appendix IV). Low number of samples and high average number of singletons may have contributed to the high zone estimates. The estimators particularly overestimated the richness of the species poor zone 2.2.

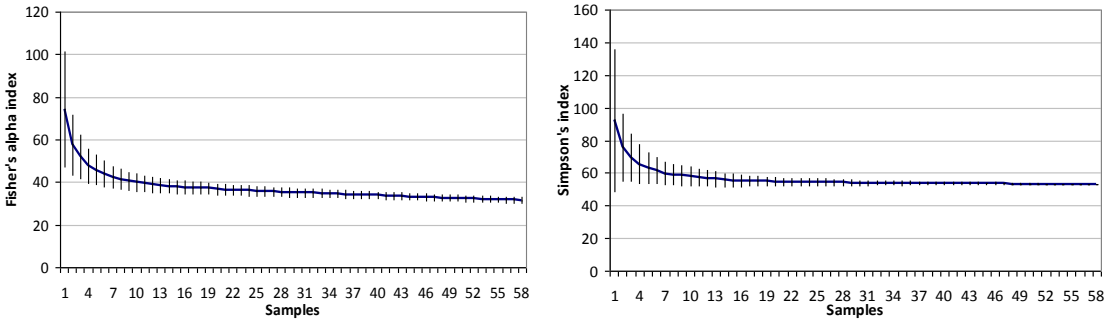


Fig. 28 Fisher's alpha and Simpson index for increasing number of epiphytic bryophyte samples collected on the *Weinmannia* host.

4.2.3 Species abundance

The bryophyte community supported by the *Weinmannia* host approximates a log normal distribution of abundance (Fig. 29).

The different composition and frequency of species within zones, readily apparent from the species transition table (Table 8), are also reflected in the varied slopes of rank-abundance plots for each zone (Table 10). Zone 3 community plot had the least steep slope, 0.014. It is also the most species rich microhabitat community on this host. The rank-abundance plot for zone 5 had the steepest slope. Zone 5 was identified to have the least stable microclimate.

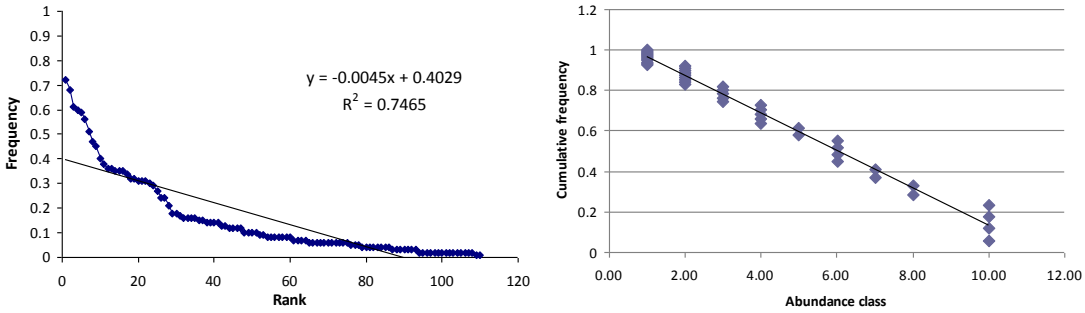


Fig. 29 Rank-abundance plot for the bryophyte community on the *Weinmannia* sp. and a cumulative frequency-abundance class plot (Gray, 1981) demonstrating the normal distribution of the collected species abundance data.

Table 10. Slope of a linear regression of rank (x) on frequency of occurrence (abundance) in zone samples (y).

Zone	Slope	R^2
1	0.020	0.87
2.1	0.016	0.88
2.2	0.021	0.76
3	0.014	0.87
4	0.017	0.81
5	0.026	0.89

4.2.4 Microhabitat communities

Colwel and Coddington's (1994), Jaccard index based, beta diversity estimate C_T for the *Weinmannia* was 116.8[6]. Whittaker's β_w for turnover of species between zones was highest in zone 2.2, and lowest in zone 3 ($\beta_{w\ all}$ in Table 11). These zones also had the lowest and highest specie richness, respectively. The C_T for turnover among the hepatics was 79.8 and lower for mosses, 37.

[6] $C_T = \Sigma b+c-2a / n$, where a is the number of shared species, b and c are species richness of samples, n is the number of samples.

Table 11. Whittaker's estimate for turnover within zones ($\beta_{w\ in\ zone}$), all species between zones ($\beta_{w\ all}$), hepatics between zones ($\beta_{w\ hep}$) and mosses between zones ($\beta_{w\ moss}$).

Zone	1	2.1	2.2	3	4	5
$\beta_{w\ in\ zone}$	2.80	2.90	4.16	3.16	3.57	2.89
$\beta_{w\ all}$	6.47	5.47	14.10	4.95	6.18	7.69
$\beta_{w\ hep}$	6.45	5.61	15.60	4.59	5.65	5.61
$\beta_{w\ moss}$	6.53	5.16	11.43	6.15	8.00	80.00

$\beta_{w\ in\ zone}$ = Mean of total number of species recorded in zone / species richness in subsample.

β_{w} = Total number of species recorded on host (all, hepatics, mosses) / mean species richness in zone (all, hepatics, mosses)

Table 12. Estimate of similarity in species composition between pairs of zones by the Jaccard and Sørensen indices.

1st	2nd	Sobs 1	Sobs 2	Shared	Jaccard	Sorensen
1	5	46	37	9	0.122	0.217
2.2	5	30	37	11	0.196	0.328
1	4	46	52	18	0.225	0.367
3	5	64	37	22	0.278	0.436
2.1	5	55	37	20	0.278	0.435
1	3	46	64	24	0.279	0.436
4	5	52	37	21	0.309	0.472
1	2.2	46	30	18	0.310	0.474
1	2.1	46	55	25	0.329	0.495
2.2	4	30	52	22	0.367	0.537
2.2	3	30	64	26	0.382	0.553
2.1	4	55	52	32	0.427	0.598
2.1	2.2	55	30	27	0.466	0.635
2.1	3	55	64	42	0.545	0.706
3	4	64	52	42	0.568	0.724

Both of the indices similarly ranked each pair of zones and agree that zones 1 and 5 had the most dissimilar species assemblages. Zones 3 and 4, and 2.1 and 3 received the highest similarity scores (Table 12). A similar indication is given by the Jaccard ranking of similarity between moss and hepatic species in each zone. Most similar moss assemblages were in zones 2.1 and the mid-crown, and on either side of the trunk (Table 13). Among the hepatics, the mid and mid-outer crown assemblages were most similar, followed by those along the sheltered side of the trunk and the mid-crown. Zones 1 and 5 were identifies as least similar for both groups.

Table 13. Ranking of similarity between assemblages of mosses and hepatics in each zone by the Jaccard index. (15 = most similar).

1st	2nd	Heps	Mosses
1	2.1	6	12
1	2.2	5	10
1	3	4	8
1	4	2	6
1	5	1	1
2.1	2.2	12	**14**
2.1	3	**14**	**15**
2.1	4	13	9
2.1	5	7	4
2.2	3	10	11
2.2	4	11	7
2.2	5	3	2
3	4	**15**	13
3	5	8	3
4	5	9	5

Comparison of lower and upper trunk assemblages within zones 2.1 and 2.2 revealed a high similarity between the two lower sections. The two upper sections were less similar than lower and upper species assemblages on the same side of the trunk (Table 14).

Table 14. Jaccard and Sørensen estimates of similarity between upper and lower trunk species assemblages.

1st	2nd	Sobs 1	Sobs 2	Shared	Jaccard	Sorensen
2.1L	2.2U	40	18	14	0.32	0.48
2.1U	2.2U	40	18	16	0.38	0.55
2.1U	2.2L	40	24	18	0.39	0.56
2.2L	2.2U	24	18	12	0.40	0.57
2.1L	2.1U	40	40	24	0.43	0.60
2.1L	2.2L	40	24	20	0.46	0.63

4.2.5 Classification of sites

No species were recovered from site 2.16 on the exposed side of the trunk. Site 2.16 was excluded from the classification analyses. The dendrogram was trimmed at approximately 20% of information (Fig. 30). The five groups closely corresponded to the arbitrarily

imposed division of the crown and trunk into Johansson zones. First to separate was site 2.20 from the exposed side of the trunk. Just 3 infrequently found species were recovered from this sample. All of zone 5 sites were clustered together into group 2. Group 3 was a mixture of mid-crown and mid-outer crown sites and 4 sites from the sheltered side of the trunk. All but two zone 2.2 sites and five zone 2.1 sites were separated into group 4, representing the majority of the trunk sites. All of the sites in zone 1 separated together into group 5. The lowest of the sheltered trunk sites was also included in this group.

Zones were also classified based on the frequency of species incidence (Fig 30). The resulting dendrogram is a summary of the site classification. The six zones were separated into 2 groups: the trunk and the crown. Zones 2.1 and 2.2 were clustered together within the trunk group. Zones 3 and 4 were separated from zone 5, but failed to separate from each other.

4.2.6 Species classification and ordination

The species classification was trimmed at 37% resulting in 8 groups (Fig. 31). Group 1 were high light specialists with a predominantly outer crown distribution. Zone 5 exclusive species, including *Frullania stenostipa*, *Lejeunea* sp. 2 and *Brachiolejeunea spruceana* were clustered in the upper half of the group. Group 2 consisted of low light species with predominantly zone 1 distribution. The upper section included species exclusive to zone 1, like *Riccardia smaragdina* and *Rhyzogonium novae-hollandiae*. Group 3 were predominantly trunk epiphytes with a range that extends into the mid-crown. Group 4 consisted of species predominantly found in the mid to mid-outer crown. Groups 4, 5 and 6 were a mixture of species most frequently found in zone 3 and 4. Group 6 was made up of species with highest frequency in zone 4, like *Macromitrium podocarpi* and *Amphilejeunea reflexistipula*. Group 7 predominantly included species found in zone 4, but had a broad distribution extending to the mid-crown and the upper trunk. This group included *Frullania brasiliensis*, *F. densifolia* and *F. riojaneirensis*. Group 8 was made up of species with a broad distribution throughout the host. The uppermost section of the group included species most frequently found in zone 2.1, like *Plagiochila stricta* and *Porotrichum longirostre*.

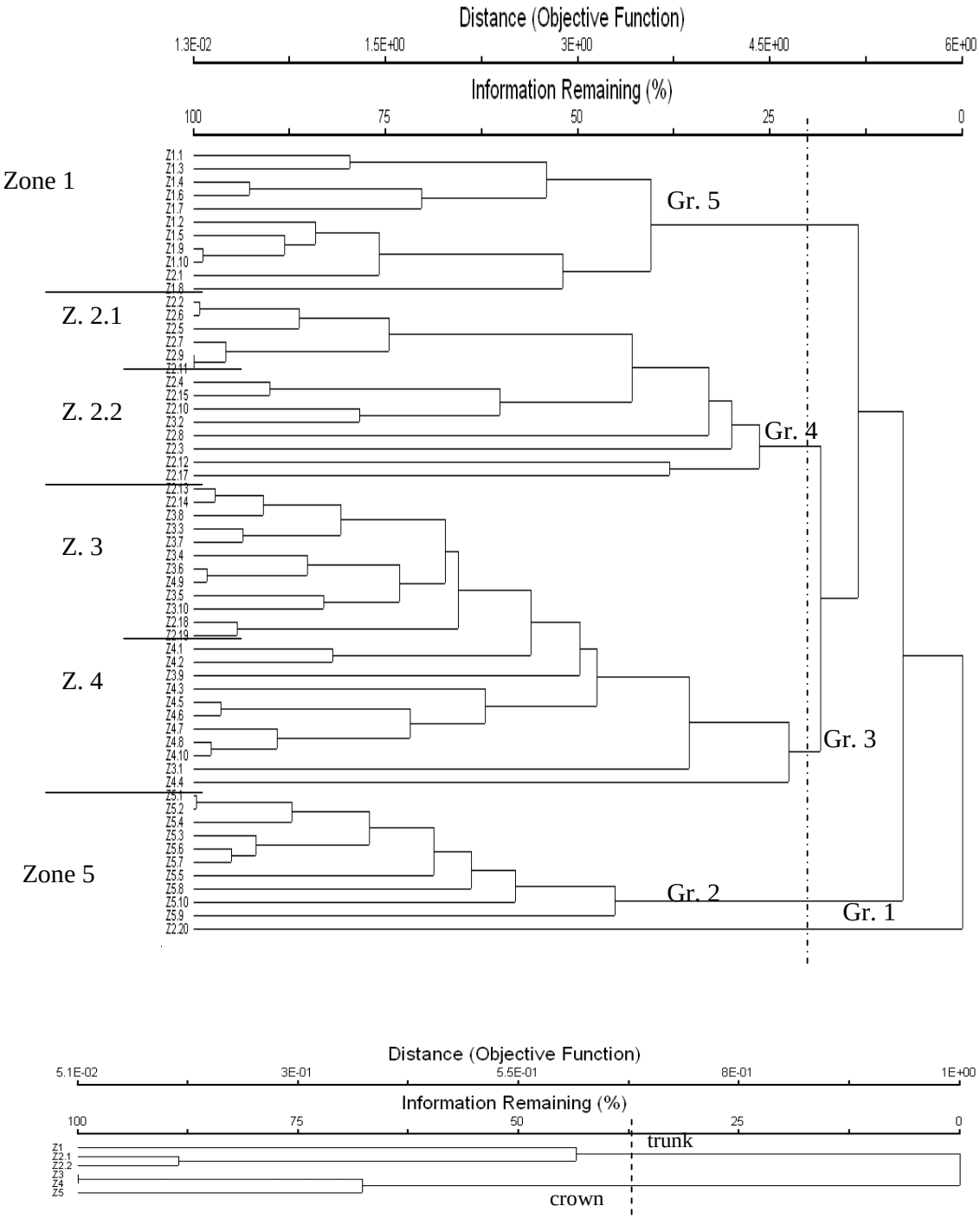


Fig. 30 Above - Classification of sample sites by similarity in species composition (Bray-Curtis, group average linking, chaining = 12.8%); Below - Classification of zones by similarity of species frequency in zones (Bray-Curtis, furthest neighbour linking, chaining = 0%).

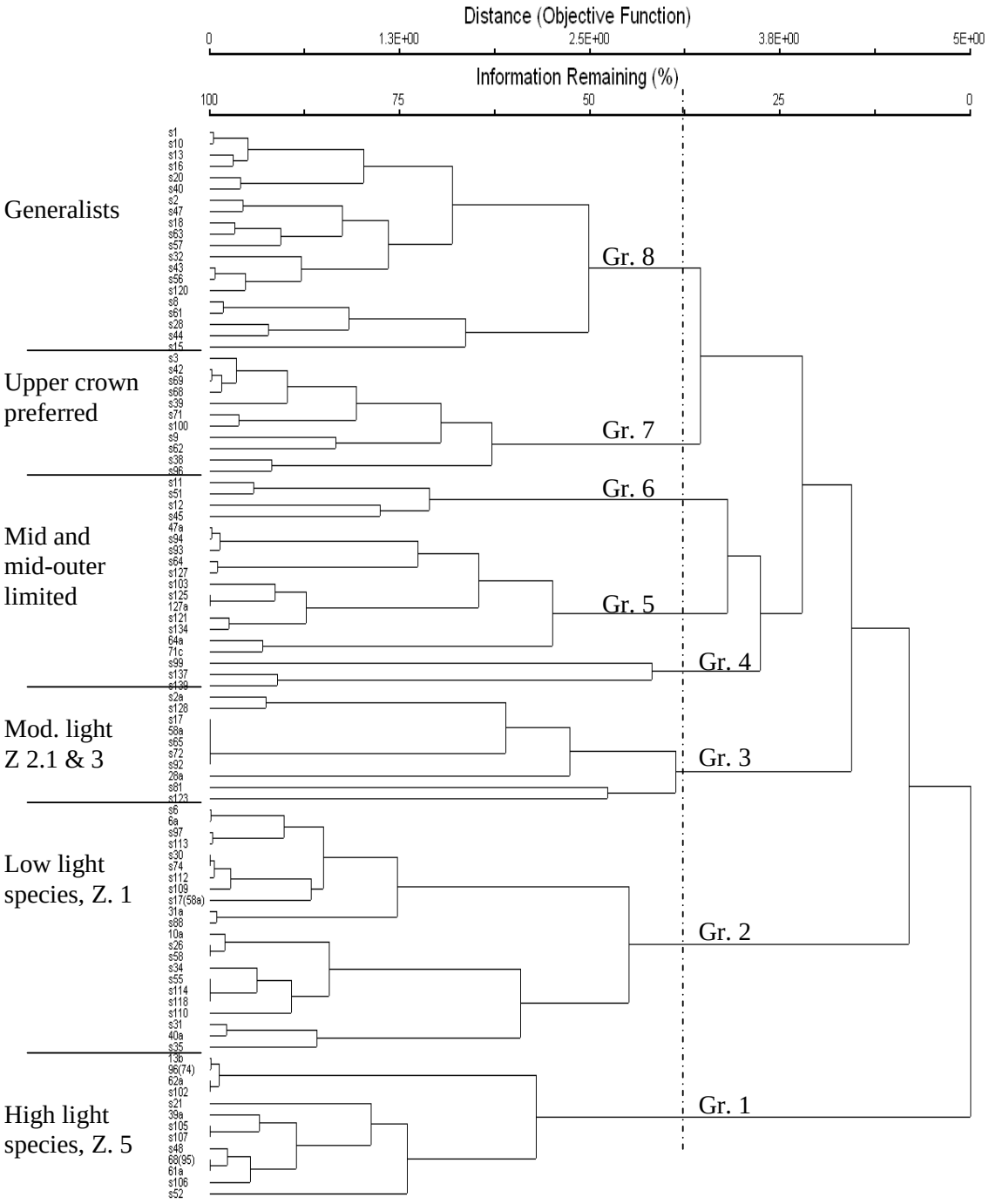


Fig. 31 Classification dendrogram of a reduced species database (Bray-Curtis, group average linking, chaining = 3.41%). For species names see Appendix V.

Non-metric multi-dimensional scaling of the species data based on occurrence across similar sites resulted in a 3 dimensional solution with a moderately high stress of 20.61 (Fig. 32). The ordination plot reflects the frequent overlap of species distributions apparent in Table 8, but some trends can be interpreted with the aid of zone exclusive taxa and species frequency values. Outer crown exclusive species and those with a clearly outer crown preference are clustered in the upper section of the plot. Species with a preference for the mid-outer and mid-crown are clustered together in the centre. Lower trunk species occupy the centre-right of the plot and the trunk species are in the lower left.

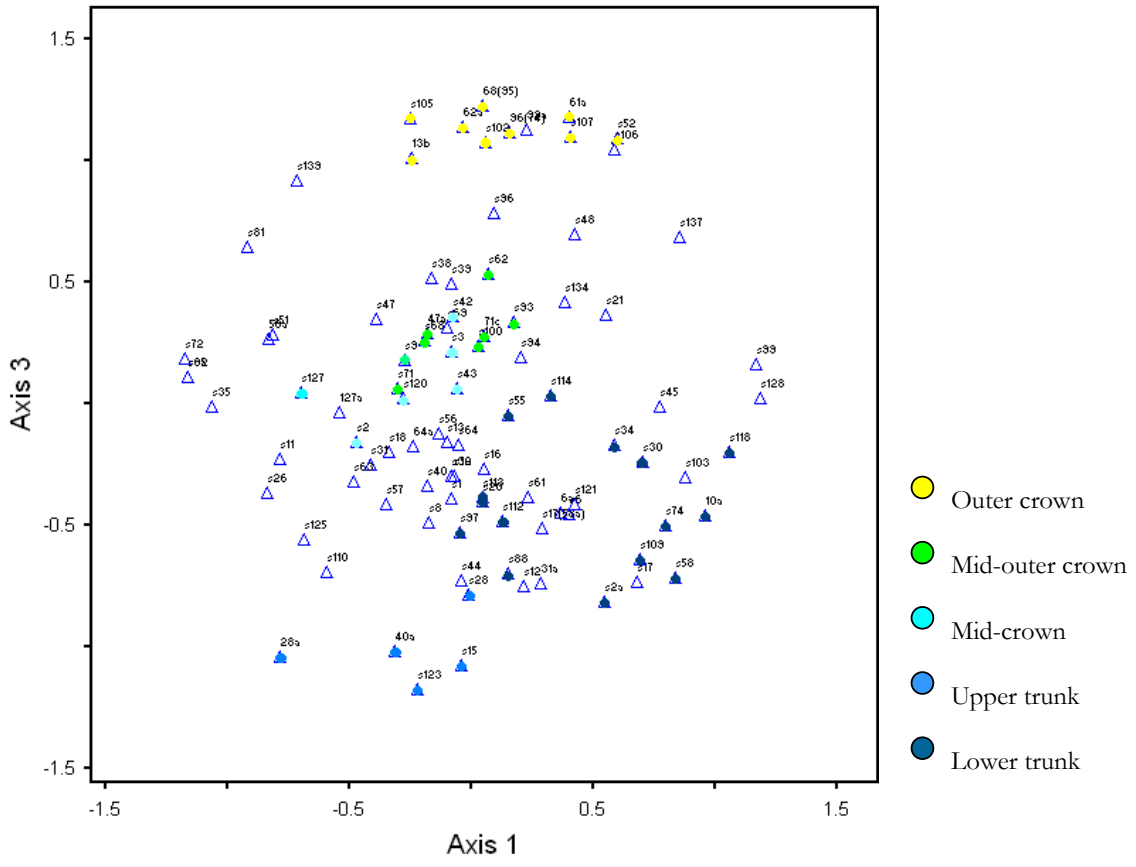


Fig. 32 NMS plot of species based on occurrence across similar samples of epiphytic bryophytes on a *Weinmannia* sp. host. For species names see Appendix V.

4.2.7 Epiphytic communities

The species found on the *Weinmannia* host formed four communities related to crown section and the height above the ground: i) the outer crown community inhabiting zone 5, ii) the mid and mid-outer crown community in zones 3 and 4, iii) the upper trunk community in zones 2.1 and 2.2, iv) the lower trunk community in zone 1.

Table 15. The outer-crown community

Frullania stenostipa-Lejeuneaceae sp. 2 **Outer crown community**	
Exclusive species	**Freq.**
Lejeuneaceae sp. 2 *	0.8
Frullania stenostipa *	0.7
Frullania sp. 5	0.4
Diplasiolejeunea sp.	0.4
Aureolejeunea fluva	0.3
Chielolejeunea subgen. *Strepsilejeunea* sp. 2	0.3
Anopolejeunea conferta	0.2
Colura tenuicornis	0.1
Drepanolejeunea araucariae var. *araucariae*	0.1
Lejeunea subgen. *Lejeunea* sp. 3	0.1
Accompanying species	**Freq.**
Harpalejeunea sp. *	1
Frullania riojaneirensis *	1
Frullania brasiliensis	0.9
Brachiolejeunea spruceana *	0.8
Drepanolejeunea infundibulata	0.8
Frullanoides densifolia subsp. *densifolia*	0.8
Omphalanthus filiformis	0.8
Macrolejeunea pallescens fo. *lancifolia* *	0.7
Oryzolejeunea sp. (ad aff *O. venezuelana*)	0.5
Microlejeunea colombiana	0.5
Cheilolejeunea comans	0.5
Frullania apiculata	0.3
Ceratolejeunea deciscens	0.3
Daltonia longifolia	0.3
Lejeunea subgen. *Lejeunea* sp. *2*	0.2
Lejeunea subgen. *Lejeunea* sp. 1	0.2
Plagiochila bifaria	0.2
Macrolejeunea pallescens	0.2
Amphilejeunea reflexistipula	0.1
Frullania subgen. *Frullania* sp. 1	0.1
Dendroceros crispus	0.1
Odontolejeunea lunulata	0.1
Zygodon reinwardtii	0.1
Lepidolejeunea eluta	0.1
Plagiochila sp. 1	0.1
Lejeunea subgen. *Nanolejeunea* sp.	0.1
Metzgeria decipiens	0.1

* - indicator species

Perhaps the most strikingly different assemblage of species is the outer crown community (zone 5) (Table 15). The community occurred on twigs to 35 mm at an average height of 23.15 m. It was made up of 35 hepatics and just 2 moss species. A mean of 14.3 species were found in samples collected in the outer crown. Identification of one of the defining species for this community was problematic beyond the family level and remains here as Lejeuneaceae sp. 2.

Fig 33. The high light specialist *Colura tenuiconis*, ventral view.

Table 16. The mid-crown community

Leptoscyphus porphyrius-Macromitrium aureum **Mid-crown community**	
Exclusive species	**Freq.**
Leptoscyphus porphyrius	0.4
Plagiochila sp. 5	0.35
Plagiochila sp. 2	0.3
Squamidium livens	0.25
Lejeunea sp. 3	0.2
Meteorium illecebrum	0.15
Macromitrium podocarpi	0.15
Ceratolejeunea maritima	0.15
Aneura pinguis	0.15
Streptopogon calymperes	0.1
Plagiochila sp. 4	0.1
Leptoscyphus physocalyx	0.1
Trachyxiphium variable	0.05
Syrrhopodon graminicola	0.05
Squamidium leucotrichum	0.05
Mnioloma cyclostipa	0.05
Macromitrium longifolium	0.05
Lophocolea trapezoidea	0.05
Brachymenium consimile	0.05
Accompanying species	**Freq.**
Frullanoides densifolia subsp. *densifolia* *	1
Frullania brasiliensis	0.95
Omphalanthus filiformis	0.95
Cheilolejeunea comans	0.85
Macromitrium aureum *	0.8
Macrolejeunea pallescens	0.75
Radula montana	0.75
Neurolejeunea breutelii *	0.7
Plagiochila bifaria	0.7
Drepanolejeunea infundibulata	0.65
Lepidolejeunea eluta	0.6
Porotrichum longirostre	0.55
Oryzolejeunea sp. (ad aff *O. venezuelana*)	0.5
Taxilejeunea pterigonia	0.5
Plagiochila sp. 3	0.45
Zygodon reinwardtii	0.45
Lejeunea subgen. *Lejeunea* sp. 1	0.45
Meteorium remotifolium	0.45
Prionodon densus	0.4
Plagiochila stricta	0.4
Papillaria imponderosa	0.35
Harpalejeunea sp.	0.35
Frullania riojaneirensis	0.35
Plagiochila sp. 1	0.3
Lejeunea subgen. *Lejeunea* sp. *2*	0.3
Metzgeria decipiens	0.3
Lejeunea subgen. *Nanolejeunea* sp.	0.25
Trichocholea filicaulis	0.2
Dicranolejeunea axillaris	0.2
Dendroceros crispus	0.15
Riccardia metzgeriaeformis	0.15
Trichostomum brachydontium	0.15
Frullania subgen. *Frullania* sp. 1	0.1
Daltonia longifolia	0.1
Mittenothamnium reptans	0.1
Lejeuneacea Tribe *Lejeuneae* sp. 1	0.1
Brachiolejeunea spruceana	0.05
Amphilejeunea reflexistipula	0.05
Microlejeunea colombiana	0.05
Frullania apiculata	0.05
Lepidopilum caviusculum	0.05
Brachiolejeunea leiboldiana	0.05
Leiomela bartramioides	0.05
Zygodon gracillimus	0.05
Zygodon obtusifolius	0.05
Lepidopilum scabrisetum	0.05
Acrobolbus antillanus	0.05
Lepidolejeunea spongia	0.05
Plagiochila sp. 6	0.05
Porotrichum substriatum	0.05
Trachyxiphium subfalcatum	0.05
Pallavicinia lyellii	0.05
Lophocolea sp.	0.05
Lejeunea sp. 2	0.05
Lophocolea coadunata	0.05

* - indicator species

The mid-crown community was the most species rich assemblage on the *Weinmania* host (Table 16). It included 74 bryophytes, 50 hepatics and 24 moss species. The mean height above the ground of the community was 20.1 m and the collections were made on branches with a mean diameter of 0.08 m. The mean number of species found in samples was 20.

The *Macrolejeunea pallescens-Prionodon densus* community spanned both sides of the upper trunk, although the exposed south-western side had a much reduced species representation and cover (Table 17). A mean of 14 species per sample were found on the upper trunk; 20.1 on the sheltered side and 7.8 on the exposed side. The mean height of the community was 8 m above the ground and the mean trunk diameter was 0.37 m. The community included 56 species, 17 mosses and 39 hepatics. There was a large overlap of species with the *Leptoscyphus porphyrius-Plagiochila* sp. 5 community in the mid-crown and the lower trunk community. The assemblage on the lower trunk was differentiated by the infrequent

Table 17. The upper trunk community

Macrolejeunea pallescens-Prionodon densus
Upper trunk community

Exclusive species	**Freq.**
Sematophyllum galipense	0.1
Leptolejeunea elliptica	0.1
Plagiochila sp. 9	0.05
Cephaloziella granatensis	0.05
Accompanying species	**Freq.**
Macrolejeunea pallescens	0.9
Prionodon densus *	0.8
Plagiochila stricta	0.75
Porotrichum longirostre	0.7
Lejeunea subgen. *Lejeunea* sp. *2*	0.65
Omphalanthus filiformis	0.6
Meteorium remotifolium	0.55
Lejeuneacea Tribe *Lejeuneae* sp. 1	0.55
Dicranolejeunea axillaris	0.5
Zygodon reinwardtii	0.45
Radula montana	0.45
Taxilejeunea pterigonia	0.4
Plagiochila sp. 1	0.35
Cheilolejeunea comans	0.35
Metzgeria decipiens	0.35
Mittenothamnium reptans	0.35
Plagiochila sp. 3	0.3
Harpalejeunea sp.	0.3
Lepidolejeunea eluta	0.3
Lejeunea subgen. *Nanolejeunea* sp.	0.3
Frullania brasiliensis	0.25
Leiomela bartramioides	0.25
Zygodon gracillimus	0.25
Thuidium peruvianum	0.25
Neurolejeunea breutelii	0.2
Frullanoides densifolia subsp. *densifolia*	0.2
Hypopterigium tamarisci	0.2
Prionolejeunea decora	0.2
Drepanolejeunea infundibulata	0.15
Lejeunea subgen. *Lejeunea* sp. 1	0.15
Lepidopilum caviusculum	0.15
Zygodon obtusifolius	0.15
Trichostomum brachydontium	0.15
Macromitrium aureum	0.1
Plagiochila sp. 7	0.1
Plagiomnium rhynchophorum	0.1
Metzgeria leptoneura	0.1
Macrolejeunea pallescens fo. *lancifolia*	0.05
Odontolejeunea lunulata	0.05
Riccardia metzgeriaeformis	0.05
Papillaria imponderosa	0.05
Trichocholea filicaulis	0.05
Frullania riojaneirensis	0.05
Daltonia longifolia	0.05
Plagiochila bifaria	0.05
Lepidopilum scabrisetum	0.05
Acrobolbus antillanus	0.05
Lepidolejeunea spongia	0.05
Plagiochila sp. 6	0.05
Porotrichum substriatum	0.05
Prionolejeunea equitexta	0.05
Plagiochila aerea	0.05

* - indicator species

exclusive taxa and the dominance structure. *O. filiformis* was less frequent than higher in the crown, as were *Frullania* species and *Radula montana*. The upper trunk community was less species rich than the mid-crown assemblage, but the sheltered, north-easterly side trunk was thickly covered with epiphytes

.

The *Riccardia smaragdina-Rhizogonium novae-hollandiae* community on the lower trunk was the second most distinct assemblage supported by the *Weinmannia* host (Fig. 34). As expected, this community included a large proportion of facultative epiphytes (80.4%), more than any other community on this host. Just two of the exclusive species,

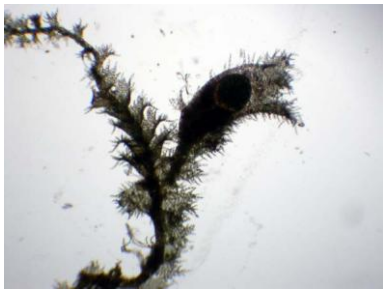


Fig. 34 The decorative *Lophocolea muricata* with perianth. One of the species only found on the lower trunk.

Table 18. The lower trunk community

Riccardia smaragdina-Rhizogonium novae-hollandiae **Lower trunk community**	
Exclusive species	**Freq.**
Riccardia smaragdina *	0.6
Rhizogonium novae-hollandiae	0.5
Jubula pensylvanica subsp. *bogotensis*	0.4
Lophocolea muricata	0.4
Plagiochila harrisana	0.3
Fissidens serratus	0.2
Plagiochila sp. 8	0.2
Trichocholea flaccida	0.2
Monoclea gottschei	0.1
Lepidozia caespitosa	0.1
Holomitrium arboreum	0.1
Accompanying species	**Freq.**
Lejeunea subgen. *Nanolejeunea* sp. *	1
Macrolejeunea pallescens	1
Radula montana	1
Porotrichum longirostre	1
Plagiochila stricta	0.8
Lophocolea coadunata *	0.8
Metzgeria decipiens	0.7
Lophocolea sp. *	0.7
Lejeuneacea Tribe *Lejeuneae* sp. 1	0.6
Plagiomnium rhynchophorum	0.6
Hypopterigium tamarisci	0.6
Lepidopilum caviusculum	0.5
Taxilejeunea pterigonia	0.4
Pallavicinia lyellii	0.4
Prionolejeunea decora	0.4
Lejeunea subgen. *Lejeunea* sp. 1	0.3
Mittenothamnium reptans	0.3
Dicranolejeunea axillaris	0.3
Leiomela bartramioides	0.3
Porotrichum substriatum	0.2
Trachyxiphium subfalcatum	0.2
Lejeunea sp. 2	0.2
Plagiochila sp. 7	0.2
Metzgeria leptoneura	0.2
Prionolejeunea equitexta	0.2
Ceratolejeunea deciscens	0.1
Lejeunea subgen. *Lejeunea* sp. *2*	0.1
Omphalanthus filiformis	0.1
Daltonia longifolia	0.1
Plagiochila bifaria	0.1
Prionodon densus	0.1
Meteorium remotifolium	0.1
Brachiolejeunea leiboldiana	0.1
Thuidium peruvianum	0.1
Plagiochila aerea	0.1

* - indicator species

Holomitrium arboretum and *Trichocholea flaccida*, were obligate epiphytes. The community was made up of 46 species, 15 mosses and 46 hepatics (Table 18). An average of 17 species was found in samples from the lower trunk.

4.3 Discussion

4.3.1 Species richness

The greatest species richness was found in the mid-crown. Many other studies have reported similar observations (Jarman and Kantvilas, 1995a; Gradstein *et al.*, 2001b; Kelly *et al.*, 2004). Not so common, from a temperate climate perspective, is the lower number of species on the lower trunk than on the upper trunk (zone 2.1). The lower trunk in temperate habitats often includes a thick sock of moisture and shade loving species, many of them facultative epiphytes extending up from the customary soil, rock and dead wood substrates. In the present study, zone 1 was clothed with pendulous and dendroid growth forms and loose weft species, suggesting no lack of moisture. The reason for higher species richness on the upper trunk may be the prevailing greater radiation intensity, suggested by

the overall greater richness of epiphytic bryophytes than obligate ground level dwellers in tropical rainforests[7]. Mean RH in zone 2.1 remained high (94.5%), just 3.6% less than in zone 1, while the annual mean total below radiation was 67% higher. Leon-Vargas *et al.* (2006) also report a thin cover of trunk epiphytes on the lower trunks in a Venezuelan cloud forest, attributing it to low light levels near the forest floor.

A critical evaluation of the bryophyte diversity on the *Weinmannia* host is hindered by the paucity of data on single tree bryophyte populations in general and different sampling methodology applied by most studies. However, a qualitative interpretation of other study findings suggests that the number of species supported by the *Weinmannia* is in the mid-range (Table 19).

Table 19. An overview of species capture by studies in various habitats.

Location and elevation	Forest type	Zones sampled	No. trees	Mosses	Hepatics	Total	Ref.
Peru, 2400m	Lower montane rain	1-5	1	38	72	110	Current study
Australia, ~200 m	Cool temp. rain	1-5	1			55	Jarman & Kantvilas 1995
Japan, 700 m	Premontane	1-5	1			78	Iwatsuki and Hattori 1965
Costa Rica, ~1550 m	Lower montane (wet)	3-4	3	41	67	108	Sillett *et al*. 1995****
Colombia, 1500 m	Lower montane rain	1-5	4	22	36	58	Wolf 1993
Colombia, 2500 m	upper montane rain	1-5	4	33	102	135	Wolf 1993
Colombia, 3510	Subalpine rain	1-5	4	19	63	82	Wolf 1993
Guyana, ~100 m	Lowland moist	1-5	11	28	53	81	Cornelissen *et al.* 1989
Venezuela, 2600 m	upper montane rain	1-5	12	22	66	88	Kelly *et al.* 2004
French Guiana, 150 m	Lowland moist	1-5	28	66	88	154	Gradstein et al. 1990
Costa Rica, 1550 m	Lower montane (wet)	1-5	unknown*	53	118	171	Gradstein *et al.* 1994
Costa Rica, 1550 m	Lower montane (wet)	1-5	2-3**			118	Gradstein *et al.* 2000
Costa Rica, 1550 m	Lower montane (wet)	1-5	***	56	134	190	Gradstein *et al.* 2000

* - the study also sampled the forest floor

** - highest average of 4 1ha plots, study sampled tree crowns and understorey vegetation.

*** - total of 4ha and 10 trees, understorey and crowns were sampled

**** - data from intact forest only

The 74 species recorded only in zones 3 and 4 is lower than the finding of Sillett *et al.* (1995), although their data included species found in three crowns and no measure of species turnover between crowns is given. Gradstein (1995) reports that the average

[7] The virtual absence of ground level bryophytes in lowland tropical rainforrest and much higher diversity found in montane forests may be related to the greater availability of light and more frequent occurrence of humus-rich soils and longer persistence of woody debris.

Gradstein SR, Pocs T (1989) Bryophytes. In "Tropical rainforest ecosystems of the world 14A'. (Eds H Lieth and MJA Werger) pp. 311-325. (Elsevier: Amsterdam)

, Gradstein SR (1995) Diversity of Hepaticae and Anthocerotae in montane forests of tropical Andes. In 'Biodiversity and conservation of neotropical montane forests'. (Eds SP Churchill, H Baslev, E Forero and L Lutyen) pp. 321-334. (New York Botanical Garden: New York) .

number of hepatics on four trees in lower montane rainforest is 46 and in upper montane rainforest 86, the latter appears quite attainable at the El Cedro site, despite the lower elevation.

MMRuns provided the best early estimate of totals species richness, while the Bootstrap estimator was less useful and closely followed the observed species number throughout the curve. The influence of more exhaustive sampling on estimator accuracy is demonstrated by their poor performance in predicting the species richness for zone 2.2. More than 50% of the species found in zone 2.2 were only found once, resulting in an estimate 77% higher than the number of observed taxa. The mean predicted species richness for the host, just 10 species more than collected, may be an underestimate as 15 singleton species still remained at the end of sampling and the species accumulation curve was still rising. The 15 could represent truly infrequent species or be indicative of insufficient sampling effort to reveal the true total species richness, despite the contrary indications by the Fisher's alpha and Simpson indices.

Many studies report a high level of variability among samples of epiphytic bryophytes, but less among hosts in a given environment (Schuster, 1957; Oksanen, 1988; Wolf, 1994). Turnover of species within zones was smaller in this study than the turnover between zones (Table 11). Estimates of variability or in the total species richness provided by many previous studies of epiphytic bryophytes may be biased due to low sample effort. The present study appears to be the most detailed floristic plot examination of a single host, which is reflected in the high number of species observed. Most recent methodologies employed just 4-10 samples per tree, sometimes not including the entire altitudinal range of hosts (Wolf, 1993b; Gradstein *et al.*, 2001b; Kelly *et al.*, 2004). Sixty samples were collected in the present study. It is not surprising that high between sample variability was found in earlier research, given the demonstrated richness of environmental gradients on each host and the low sampling effort. The focus on sampling many trees rather than more thoroughly sampling fewer individuals goes against the conclusions reached by early studies about sample variability. If the study objective is to reveal species diversity, why sample many trees that have a lower turnover than a single host.

Sillett *et al.* (1995) found 109 species in the mid-crown sections of three *Ficus* spp. near the Monteverde cloud forest reserve, while the highest number of species captured by Gradstein *et al.* (2001) over a hectare within the reserve, including sampling from 2-3 trees, was 118. Gradstein *et al*. (2001) claim that species area curves indicated that just two of four 1 ha plots yielded 75% of the total diversity. Surely, 75% of the total 190 bryophyte species found by the study, but not likely total diversity for the entire study area, not to mention the reserve. The report quotes Wolf's (1993a) estimate of 75% species capture on just four trees. Wolf used 10 samples in each tree, ranging from 'a few to 20 dm^2'. His claim of 75% capture of total species diversity for even a small landscape unit with the reported sampling effort may be an underestimate. Further discussion of sample size and species capture is presented in the concluding chapter 6.

4.3.2 Hepatic to moss ratio

The community structure, in terms of species richness and volume on the *Weinmannia*, is driven by hepatics. The overall hepatic to moss ratio of 2.44 is comparable to the 2:1 ratio found along a transect in Chachapoyas, northern Peru, stretching from 1200-3200 m (Frahm, 1987) and 2.4 found by Gradstein *et al.* (2000) in Monteverde, Costa Rica. Wolf (1993) also notes the dominance of hepatics along his Colombian transect spanning more than 3000 m in elevation, adding support to the hypothesis that overall contribution of hepatics to bryophyte diversity increases with humidity. The proportion of hepatics is smallest in zone 2.2, the exposed side of the trunk, shown to be warmer and drier than the more species-rich sheltered side. Gradstein and Pócs (1989) report opposing dominance trends of mosses and hepatics on the moist and dry sides of a range near Santa Rosa de Cabal, Colombia. Hepatics were more numerous in the moist environment, while mosses dominated on the dry side.

Hepatic to moss ratios as high as 4:1 for individual hosts have been found by the author in cool temperate cloud forest near the wet coast of western Tasmania (~ 1000 m, mean annual precipitation 3839 mm, RH 92.3). The similarity in the type of epiphytic species found in comparable sections of the Tasmanian hosts suggests that a common set of

environmental parameters may be driving the variation in species composition in cool temperate and tropical montane cloud forests.

The relationship between humidity and hepatic species richness does not explain the lack of moss species in zone 5, on average, one of the least humid parts of the tree. Hepatic dominance in the outer crown has also been noted in other studies. Most common twig species across a range of forest types are small Lejeuneaceae, with appressed habits and frequently lobed leaves, credited with enhanced extracellular water storage capacity that prolongs their physiological activity before dehydration in this highly irradiated environment (Iwatsuki, 1960; Proctor, 1981; Jarman and Kantvilas, 1995a; León-Vargas *et al.*, 2006). One of the characteristics of upper montane cloud forest that helps to distinguish it from lower montane communities is the outer canopy abundance of fruticose lichens and the pendulous habit adopted by some species like *F. riojaneirensis* (Wolf, 1993a). Both of these characteristics have been associated with habitats that experience frequent cycles of dehydration and rehydration (Norris, 1990; Frahm, 1994; Proctor, 2004). Just two mosses were found in the outer crown. *Zygodon reinwardtii* and *Daltonia longifolia* are small, obligate epiphytes. However, fruticose lichens were abundant (Fig. 25). These indicators correlate with microclimatic observations introduced in chapter 3 and suggest that frequent cloud and the mechanism behind its capture (Chang *et al.*, 2006) may be responsible for shaping the community structure and species habit in zone 5, masked by the low RH average.

4.3.3 Abundance, competition and disturbance

The patterns of diversity recorded along the altitudinal micro-gradient offered by the *Weinmannia* host appear to have a parallel in patterns of species distribution over much larger altitudinal ranges. Wolf (1993a) explained the peak of bryophyte diversity identified between 2550 and 3190 m as an interaction of mass effect, ecological equivalency and species range overlap, apart from the affects of niche relations and habitat diversity. The ecotonal zone referred to by Wolf (1993a) is not dissimilar to the mid-crown zone 3 of the *Weinmannia*, where both crown and trunk species' ranges overlap.

The mass effect hypothesis requires a nearby propagule rich centre from which new individuals can readily colonise available niche space (Shmida and Wilson, 1985). Bryophytes produce copious volumes of readily transportable propagules, evidenced by the much broader ranges among bryophyte species in the Neotropics than recorded for vascular flora (Gradstein *et al.*, 2001a). The epiphytic environment is also likely to be dynamic due to disturbance by bark exfoliation, branch fall, epiphytic clump slumping and animal interactions (Nadkarni and Matelson, 1989; Wolf, 1993a; Catchpole, 2004), providing new colonisation opportunities. The effect of ecological equivalency should be greatest in patchily distributed habitats (not unlike branches) and where competitive interactions are reduced (Shmida and Wilson, 1985). Although no data are available about competitive replacement rates of tropical epiphytic bryophytes, investigations of terrestrial communities in temperate habitats suggest that a competitive equilibrium is not reached (Slack, 1977; Watson, 1980) and that competitive interaction between bryophyte species is not strong (During and ter Horst, 1987; During and van Tooren, 1988). High within-habitat variability noted for epiphytic bryophytes (Russell and Miller, 1977; Oksanen, 1988) has led some to suggest that epiphytic communities may be composed of ecologically near equivalent species (Schuster, 1957; Slack, 1977) randomly colonizing available niche space (Wolf, 1994). The low slope of the rank-abundance plot for zone 3 and the tree as a whole is characteristic of just such a community (Magurran, 2004).

Zone 5 was repeatedly identified by statistical analyses as different from the other sections of the host. This is also demonstrated by the sharp rise in obligate epiphyte species, the reversal of the temperature and RH gradients and the highest proportion (27%) of zone faithful species. The rank-abundance plot of its community also had the highest slope, suggesting the prevalence of demanding conditions that favour a few specialist taxa. Overall, the ranking of the rank-abundance plot slope may be interpreted as a stress gradient imposed by habitat characteristics on bryophyte species. The order of increasing slope (demanding growing conditions) for zones was: 3<2.1<4<1<2.2<5.

4.3.4 Epiphytic communities

Four communities were recognised in the present study, although their boundaries are different from those of epiphytic communities described in earlier studies. Wolf (1993b; 1993c) described 20 epiphytic communities along his Colombian transect, based on ordination of the species and environmental data. The communities were separated by altitude and height within the hosts into canopy and tree base communities. Kelly *et al.* (2004) in Venezuela divided the epiphyte assemblage into 3 communities - the tree bases, trunks and major branches, and minor branches and twigs, corresponding to zone 1, zones 2-3 and 4-5 respectively. Unlike the present study, Kelly *et al*. and Wolf investigated the distribution of vascular and non-vascular species, including lichens. As epiphytes, each of these floristic groups displays different distribution and abundance characteristics. Lichens generally dominate the outer crown, preferring habitats with high radiation intensity and low relative humidity (Hosokawa *et al.*, 1964; Clement and Shaw, 1999). Bryophytes require less light and thrive in moist conditions. Highest species richness and abundance is generally found in the mid-crown (Gradstein *et al.*, 2001b). Vascular epiphytes generally are infrequent along the trunk, but are much more diverse and in the mid and mid-outer crown (Catchpole, 2004). The spatial relationship between communities is likely to depend on the overall epiphytic species composition and the focus of the study.

The Outer crown community

This assemblage on the *Weinmannia* was similar to the *Diplasiolejeunea pauckertii* - *Brachiolejeunea laxifolia* community described by Wolf (1993b). It is comforting to note that Wolf's list also included a *Lejeunea* sp. B. Lejeuneaceae is a very large family with approximately 70 genera and hundreds of species in Latin America, many awaiting taxonomic treatment (Gradstein *et al.*, 2001a). Interestingly, Wolf reports the *D. pauckertii – B. laxifolia* community as the most species rich (76 spp.) lower montane community for that study, but fewer species were recovered per relevé (13.9) than the mean number found on the *Weinmannia* (14.3), suggesting a greater turnover along his mammoth altitudinal transect.

F. stenostipa, the second species chosen to define the outer crown community, is an obligate canopy hepatic in the subgenus *Chonanthelia*. *Frullania* in the Neotropics are generally restricted to canopy, but are also occasionally found in well illuminated sites in the forest understorey. Most taxa are strongly pigmented; a likely protective adaptation for life in the preferred strong radiation environment of the outer canopy (Gradstein *et al.*, 2001). Subgenus *Chonanthelia* are predominantly montane species, with *F. stenostipa* limited to the Andes. *C. tenuicornis* is another high light specialist (Fig. 33).

The majority of the hepatics in this community have leaves with lobules that facilitate the storage of large amounts of extracellular moisture. What perhaps is more interesting is the plastic growth form of some hepatic species in response moisture availability. *Frullania brasiliensis* grew as an appressed mat in habitats where moisture is limiting, but formed pendant mats in the outer crown stimulated by frequent presence of mist delivered by passing low clouds. A similar tendency was observed by Kelly *et al.* (2004) in a Venezuelan cloud forest. The community is rich in obligate epiphytes that include the only two moss species

The mid-crown community

The only hornwort species found in the present study, *Dendroceros crispus*, was most frequent in the mid-crown. Hornworts are infrequent throughout the Neotropics. Just one species was recorded by a recent survey in Monteverde, Costs Rica (Gradstein *et al.* 2001), two species were found by Opisso and Churchill (2007) and three species at the Reserva Biológica San Francisco in Southern Ecuador (Nöske *et al.*, 2003). The mid-crown community on the *Weinmannia* is similar in character and shares a number of key species with the *Omphalanthus filiformis* community described by Wolf (1993c). He lists *O. filiformis*, *F. brasiliensis* and *Taxilejeunea pterigonia*, also present in the mid-crown community on the *Weinmannia*, as exclusive to the upper montane belt. He notes that these species are known generalists that occasionally invade disturbed areas. This fits well with the pattern of species distribution on this host; the mid-crown was dominated by species with a wide altitudinal range within the host. A similar pattern of species presence and dominance was recorded by the author on *Athrotaxis selaginoides* and *Nothofagus*

cunninghamii (~1000 m) in temperate montane cloud forest on Mt. Hamilton in western Tasmania. Wolf's *Omphalanthus filiformis* community included 135 species, with mosses outnumbered 3.1:1. This ratio is higher than found for the mid-crown community on the *Weinmannia* and suggests generally wetter conditions along his transect. The mean number of taxa found per relevé by Wolf was 21.2, a little higher than the 20.4 for the present study.

Macromitrium and *Plagiochila* species, *Leptoscyphus porphyrius*, *Ceratolejeunea* and *Papillaria imponderosa* were common elements on the large branches in Monteverde (Gradstein *et al.*, 2001b), as in the present study, but *Bazzania* and *Herbertus* were not recorded on the *Weinmannia*. A large proportion of mid-crown species found by Sillett *et al*. (1995) and Wolf (1974) appeared to have a narrow altitudinal range within hosts, which led them to suggest that species in this section of the crown may be more specialised. The mid-crown faithful species made up 26% of the *L. porphyrius-M. aureum* community, three percent less than the proportion of faithful species in the outer crown community.

The lower trunk community

This assemblage shared a number of key taxa with the *Mittenothamnium reptans* lower trunk community described by Wolf (1993c), but it appeared quite different to the lower trunk assemblage described by Kelly *et al.* (2004). Wolf notes that *Mittenothamnium reptans* is a canopy species at elevations below 2460 m. In the present study conducted at 2400 m, it was found as high as zone 4. Wolf recorded 18% cover and a mean of 3 thalose liverworts for this community in Colombia, values higher than for the present study, again suggesting more mesic conditions at his study sites. The Colombian community included a similar number of species (49), but the mean number per relevé was 2.1 species lower than the mean per sample in the present study.

Gradstein *et al.* (2001) reports *Omphalanthus filiformis*, *Taxilejeunea pterigonia* and *Metzgeria leptoneura* as common in the understorey at the Monteverde, Costa Rica. These species were found predominantly on the trunk in the present study. *Plagionmium*

rhynchophorum and *Mittenothamnium reptans* was found on rotten logs by Gradstein *et al.* (2001). He notes that these species are also inhabit the lower trunk, as was found in the present study, but additionally, distribution of *M. reptans* extended as high as zone 4. *Pallavicinia lyellii* reported on trunk bases for Monteverde was also found in the same microhabitat at El Cedro.

4.4 Conclusion

The species recorded on the *Weinmannia* and their patterns of abundance provide a valuable insight not just into the world of bryophytes, but also offer clues about the nature of the forest itself. The site is located at 2400 m and although it has been arbitrarily assigned to the lower montane belt, the true boundary between the lower and upper montane rainforest is not defined by altitude alone. Micro-topography and local weather patterns can influence microclimate and vegetation characteristics.

The epiphytic bryophytes listed for the *Weimnannia* indicate that El Cedro is located in a transition zone between lower montane and upper montane rainforest habitats. The communities identified in the present study include some elements, like *Cloura tenicornis*, *Leptolejeunea*, *Jubula pensylvanica* subsp. *bogotensis* and *F. riojaneirensis* that are reported to be more common in the lower montane belt, while *Scapania portoricensis*, *Herbertus* sp., *Omphalanthus filiformis*, *Taxilejeunea pterigonia* and *F. brasiliensis* are more typical of the upper montane belt (Wolf, 1993c; Gradstein, 1995). Ecotonal zones, like that surveyed between 2500-3000 m along the Santa Rosa de Cabal range by Wolf (1993b; 1993c), have proven to be particularly species rich.

Bryophytes are good indicators of forest type (Gradstein, 1995; Werner *et al.*, 2005) and their community composition may also be indicative of the prevailing climatic conditions. The hepatic to moss ratio has been shown to be closely associated with the availability of free moisture (Gradstein, 1995; Jarman and Kantvilas, 1995b). The relatively low ratio of hepatics to mosses at base of the *Weinmannia*, together with the pendulous growth-form displayed by the *Frullania* species in the outer crown suggest that frequent mist,

particularly over the dry season, may be important for the maintenance of the species rich epiphyte community in the *Weinmannia*.

The Weinmannia host growing in lower montane forest on the Yanachaga-Chemillén Range, Peru, supported 110 species of epiphytic bryophytes, 78 hepatics and 32 moss species. Twenty hepatics and three mosses found on the host have not been previously recorded in Peru. This appears to be the highest single tree species richness reported in the literature to date and is an indication of the as yet poorly catalogued bryophyte species richness in the Peruvian Andes.

Chapter 5. Environmental variables and species distribution.

The variation in physiological tolerances of individual bryophyte species is reflected by their overlapping distribution along interrelated environmental gradients that exist within phorophyte hosts (Slack, 1976). Ecophysiological experiments conducted by Hosokawa *et al.* (1964) and more recently in Venezuelan cloud forests by León-Vargas *et al*. (2006) demonstrated that corticolous epiphytes growing at the base of trunks needed much less light (100 μmol m^{-2} s^{-1}) to reach their respiration compensation point than upper crown species (200 μmol m^{-2} s^{-1}). Ashton and McRae (1970) tested the desiccation tolerance of epiphytes growing on a *Nothfagus cunninghamii* and found that butt species were more easily damaged by water deficits than species typically found in the upper crown. León-Vargas *et al*. (2006) reached a similar conclusion, but also demonstrated that there were differences in the rate of recovery from different magnitudes and duration of desiccation among lower trunk and crown species. The capacity to cope with desiccation is affected by the rate of water loss, as well as the cellular repair and constitutive protection mechanisms adopted by individual species (Oliver and Bewley, 1984; Oliver and Bewley, 1997; Oliver *et al.*, 2000).

Different bark characteristics, colonisation and turnover dynamics also influence the composition of epiphytic bryophyte communities (Barkman, 1958; Sillett *et al.*, 1995). Assemblages on the same host species at locations with different climates were found to be different (Iwatsuki, 1960; Hoffman and Kazmierski, 1969), but also different hosts growing in the same environment may support a distinct assemblage of species (Schmitt and Slack, 1990; Dalton, 1998). Variation in species composition on broad leaf and conifer species has been attributed to the limitations imposed by generally higher bark acidity of conifers (Slack, 1976; Schmitt and Slack, 1990). Evidence of host fidelity was also found by Wolf (1994) among bryophytes along his Colombian transect. Different host species have a characteristic bark texture, bark water holding capacity and stability.

These variables may also change along the height and age gradients for each host (Barkman, 1958; Van Leerdam *et al.*, 1990).

The growth-form and morphology of individual species have also been correlated with microhabitat characteristics. Kürshner and Parolly (1998) investigated the water storing and conducting tissues of bryophytes along their transect in northern Peru and correlated the observed adaptations to the variation in climate over an altitudinal gradient that span from lowland to upper montane elfin forests. They found that mat growth-forms, often associated with characters like the presence of water lobules and rhizoid discs, were typical of the lowland forest, perhaps reflecting the overwhelming dominance of the Lejeuneaceae at low elevations (Gradstein, 1995). Fan, weft, dendroid and pendant growth-forms, capable of taking full advantage of the frequent precipitation and fog were more common in the montane belt. These were replaced by short and tall turfs and tail growth-forms in the sub-Andean belt.

Various environmental parameters have been suggested to influence the segregation of bryophyte species on tree hosts. Wolf (1994) identified altitude and height within the tree to be important characteristics that separated various communities. A similar conclusion was reached by Kelly *et al.* (2004) who found height above the ground and the horizontal gradient, reflecting a change in vegetation type, to be most important parameters differentiating species distribution. Sillett *et al.* (1995) found greater climatic fluctuation and lower epiphyte species richness on isolated trees than on hosts of the same species growing in intact forest. He identified a desiccation gradient as the likely cause of the variation in community structure. Studies by Hosokawa *et al.* (1964) and Tobiessen *et al.* (1977) indicated that radiation intensity and moisture may determine the vertical distribution of species in tree hosts.

Sensitivity of bryophytes to an array of habitat characteristics makes them useful indicators of habitat type and environmental change (Rao, 1982; Gradstein, 1995; Benzing, 1998; Andersson and Gradstein, 2005). The shifting hepatic to moss ratio has been correlated with variation in moisture availability (Gradstein *et al.*, 1989; Jarman and

Kantvilas, 1995b). The variation in bryophyte community composition along the microclimatological gradients that exist along each tree host may be useful as a fine gauge of local climate change. Nadkarni and Rodrigo (2002) demonstrated the utility of epiphytes as climate change indicators by transplanting vascular species along a moisture availability gradient provided by rising altitude. They found that plants transplanted to drier conditions at lower elevations had greater leaf mortality, lower growth rates and life span than plants transplanted within a given altitude. Bryophytes, lacking a protective cuticle, are even more closely linked to their environment and may more quickly respond to climatic change than vascular species.

The general lack of information about tolerances of tropical bryophytes is a major hindrance to employment of epiphytes as environmental change indicators. Studies of bryophyte phytosociology in tropical montane habitats have begun to map the distribution of species, associating communities with forest types at various altitudes and the related climate. Similarly, presence of some species at different heights within rainforests may provide information about their climate. *Mittenothamnium reptans* is reported to predominantly occur in the canopy of lower montane forests, but is more commonly found near the ground in more open upper montane cloud forests (Wolf, 1993c). The variation in abundance of individual epiphytic species over phorophyte hosts may provide an even earlier indication of changing environmental conditions.

This chapter examines the relationship between environmental parameters and distribution of bryophyte species on a mature *Weinmannia* sp. host, growing at 2400 m in lower montane rainforest, Peru, to identify which have the greatest influence on the observed pattern of species distribution and abundance. An attempt was also made to identify epiphytes with a potential to act as microclimate change indicators and reveal the environmental parameters most closely associated with their current distribution patterns. The environmental parameters tested were: height above the ground, diameter of trunk and branches, relative humidity, temperature, visible sky, leaf area index and total below, direct below and diffuse below radiation.

5.2 Results

The methods are presented in chapter 2, section 2.4.

5.2.1 Correlation between variables

Associations between the environmental variables were generally aligned with the altitudinal gradient presented by the host. Temperature, VisSky and the radiation varibles (TotBe, DirBe, DifBe) were positively correlated with increasing height above the ground, while trunk and branch diameter, RH and LAI were negatively associated. Strength of the correlations is indicated in Table 20.

Table 20. Correlation of environmental variables (Pearson's r). All associations were significant (P < 0.001).

Height – height above ground; Dia – diameter ; RH – relative humidity; Temp – temperature; VisSky – proportion of visible sky; LAI – leaf area index; TotBe - total below radiation; DirBe – direct below radiation; DifBe – diffuse below radiation.

	Height	Dia	RH	Temp	VisSky	LAI	TotBe	DirBe
Dia	-0.938							
RH	-0.943	0.926						
Temp	0.790	-0.696	-0.768					
VisSky	0.888	-0.832	-0.803	0.751				
LAI	-0.893	0.813	0.847	-0.774	-0.880			
TotBe	0.888	-0.836	-0.811	0.787	0.984	-0.861		
DirBe	0.872	-0.824	-0.801	0.789	0.959	-0.834	0.993	
DifBe	0.893	-0.838	-0.810	0.775	0.995	-0.876	0.994	0.975

Temperature (Temp) was weakly correlated with other variables. Temp had a moderate negative correlation with LAI, but was more weakly associated with VisSky. Temp also had a weak, but stronger positive relationship with DirBe than the other radiation variables and was weakly correlated with RH. VisSky and LAI had stronger associations with DifBe than DirBe or TotBe radiation. RH was most strongly associated with LAI (+ve) and TotBe (-ve). The radiation variables were strongly correlated with each other.

5.2.2 Principal components analysis

The fist PCA axis represented 87.64% of the variation in the environmental data and 99.97% of the variation was explained by 7 axes (Table 21). The comparison of eigenvalues and the Broken-stick eigenvalues (Jackson, 1993) indicates that just one axis may be worthy of interpretation. TotBe and DifBe were equally most strongly associated with Axis 1 (r = 0.97). Height, VisSky and DirBe shared a similar level of correlation with 0.96. Temperature had the lowest correlation coefficient, 0.84. RH had the strongest correlation with Axis 2 (Fig. 35).

Correlations between environmental field data and eigenvector elements for each variable were generally very weak. The strongest were those for VisSky (r = 0.706), DifBe (r = 0.628) and height above ground (r = 0.604). LAI and DirBe were most weakly associated with their corresponding eigenvector elements (Table 21).

Table 21. Above - eigenvalues for the first 9 axes of the environmental data PCA. The Broken-stick eigenvalue indicates the expected eigenvalue purely due to chance (Jackson, 1993). Below - correlation coefficients (Pearson's r) for associations between the field data and eigenvector elements for environmental variables.

AXIS	Eigenvalue	% of Variance	Cum.% of Var.	Broken-stick Eigenvalue
1	7.887	87.639	87.639	2.829
2	0.464	5.158	92.796	1.829
3	0.339	3.762	96.559	1.329
4	0.178	1.977	98.536	0.996
5	0.057	0.633	99.169	0.746
6	0.041	0.454	99.623	0.546
7	0.031	0.348	99.971	0.379
8	0.003	0.029	100.000	0.236
9	0.000	0.000	100.000	0.111

Height	Dia	RH	Temp	VisSky	LAI	TotBe	DirBe	DifBe
0.604	0.277	0.438	0.394	0.706	0.141	0.393	0.147	0.628

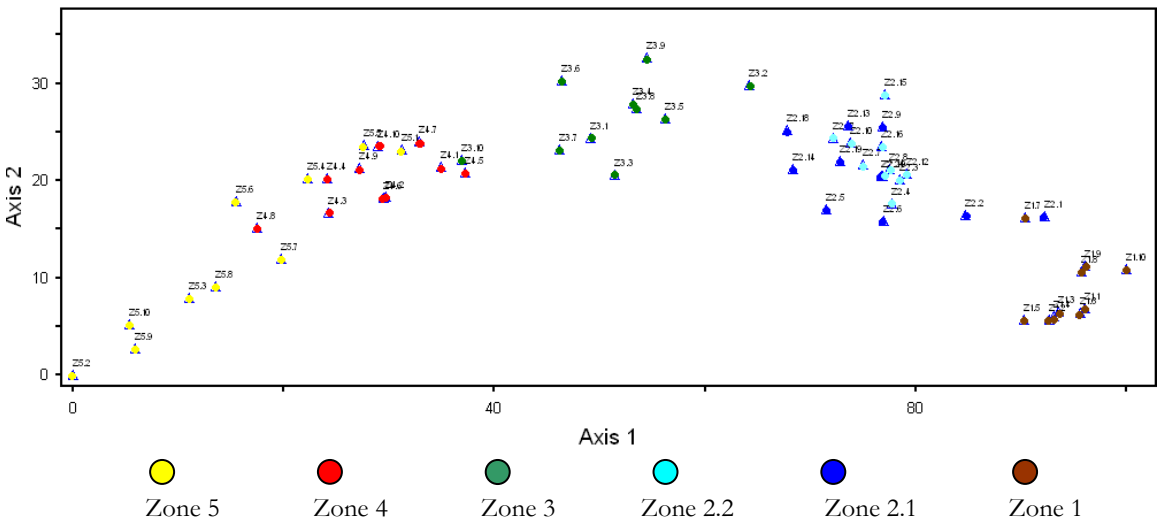


Fig. 35 Graphical representation of the variation in environmental variables among sites as generated by PCA. Total below and diffuse below radiation had equally strongest correlations with Axis 1 (r = 0.97), RH had the strongest association with Axis 2 (r = 0.36). Outer crown sites were plotted on the left side, the mid-crown sites in the centre and the lower trunk on the right.

5.2.3 Non-metric multi-dimensional scaling

The NMS ordination produced a two dimensional solution with a stress of 15.5 and final instability of 0.00005. The vectors extended in nearly opposite directions, closely aligned with the altitudinal gradient along the host. (Fig. 36). Hight above the ground had the highest correlation (r = 0.94). Along the second axis, diameter was most strongly correlated with r = 0.149 (Table 22). The variation in diffuse radiation was more strongly correlated than TotBe. Interestingly, the classic climatological variables, temperature and RH, had the lowest scores.

The lower trunk, upper trunk, mid-crown and outer crown communities were clearly defined on the NMS plot. As indicated by earlier analysis, there was more overlap between the upper trunk and mid-crown communities than other assemblages. The outlier sites, one in the upper trunk community and another in the mid-crown community, included an unusually small number of species, just 3 and 5 respectively. The upper trunk site was considerably more humid and a little cooler than the nearby trunk sites. There was nothing outstanding about the microclimate data for the mid-crown site.

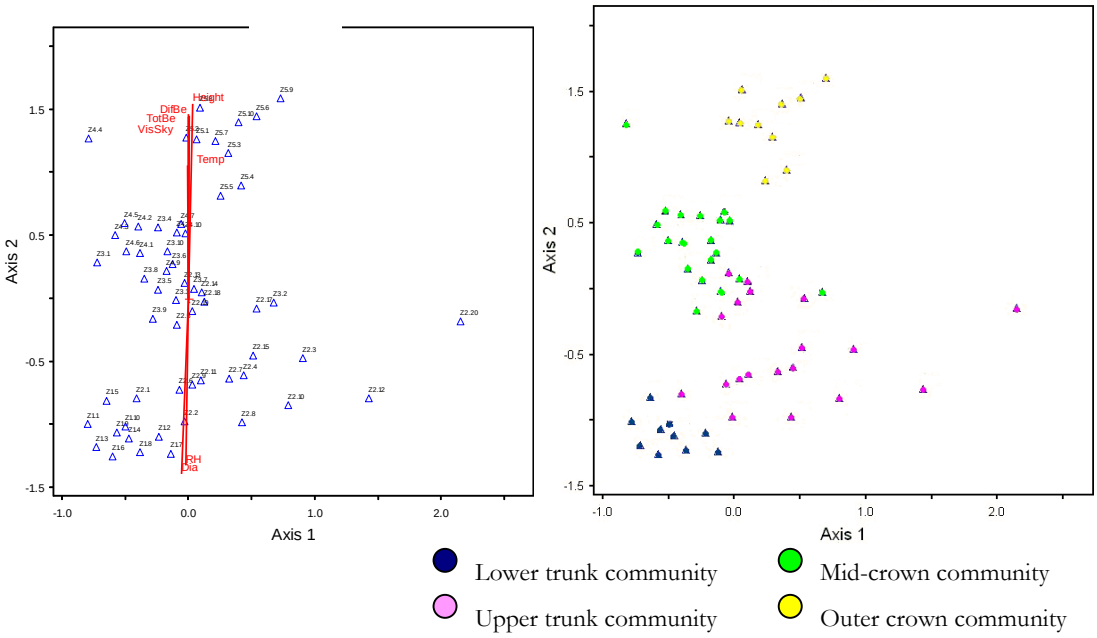


Fig. 36 Graphical representation of the relationship between species composition and environmental variables across sample sites, as interpreted by NMS ordination, with a joint plot overlay of variable vectors (left). The epiphyte communities formed well defined clusters (right).

Table 22. Highest correlations of environmental variables to the first NMS axis. Diameter had the highest correlation with the second axis (r = 0.149).

Variable	Highest r
Height	0.940
DifBe	0.919
TotBe	0.913
VisSky	0.912
Dia	0.894
RH	0.868
Temp	0.796

The subsequent NMS ordination (stress = 15.5), without the variable Height (see discussion below), produced a very similar plot and ranking for maximum correlations of the remaining environmental variables (Fig. 37). Diffuse below radiation (DifBe) had the highest correlation (r = 0.919) along axis 2 and diameter (Dia) was most strongly correlated with axis 1 (r = -0.37).

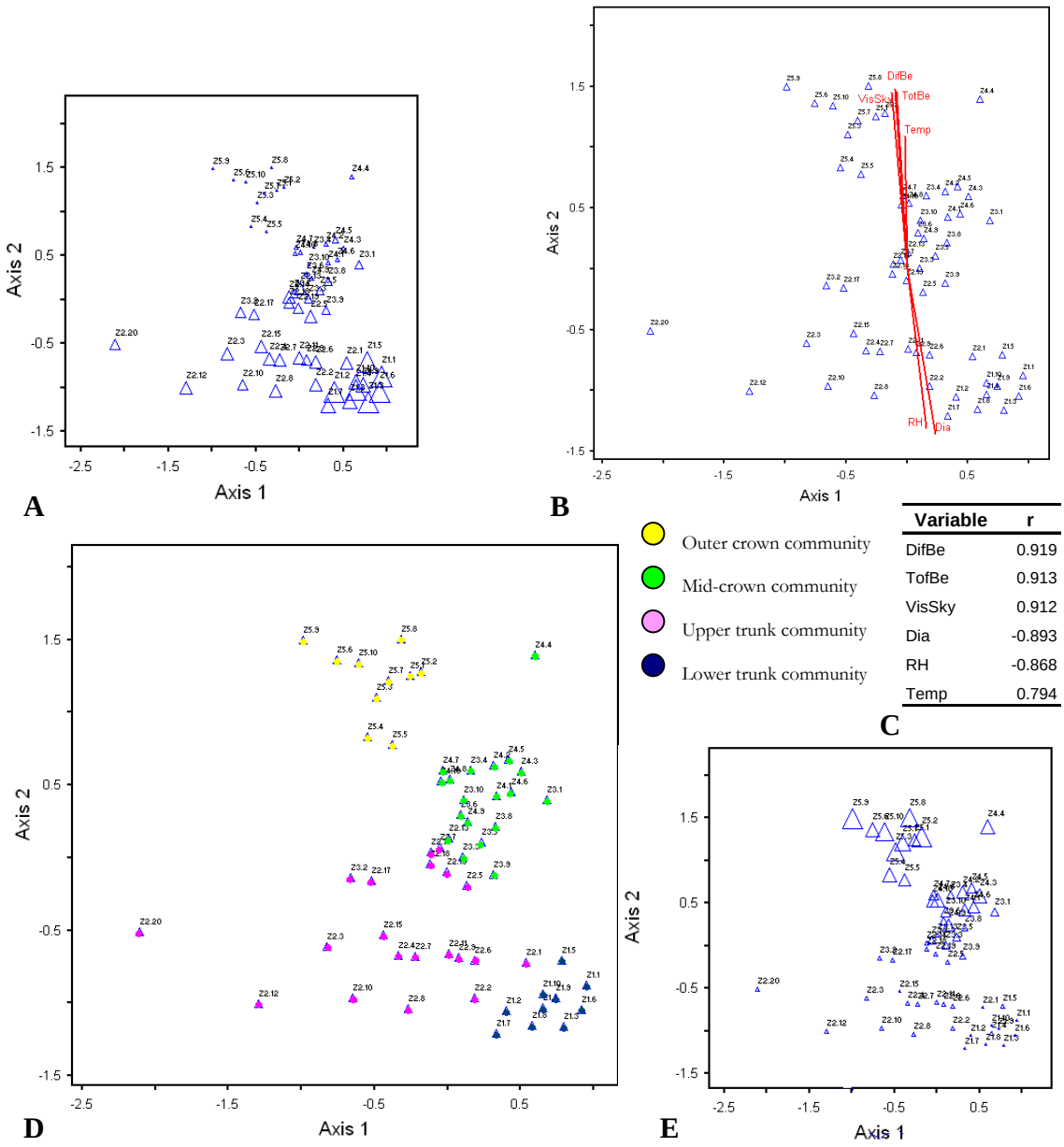


Fig. 37 NMS ordination plots representing species composition and environmental data collected on a Weinmannia sp. host in lower montane rainforest, Peru (stress = 15.5). A) Overlay for the variable diameter (Dia) most strongly correlated with axis 1 (r = -0.37); B) Vectors of the environmental variables; C) Maximum correlations (Pearson's r) for environmental variables: diffuse below and total below radiation, visible sky fraction, branch diameter, relative humidity and temperature; D) Bryophyte communities formed clearly defined clusters; E) Overlay for diffuse below radiation (DifBe) most strongly correlated with axis 2 (size of the symbol is indicative of the variable's magnitude).

5.2.4 Species - microhabitat associations

Distribution and frequency of species offer some hints about their likely habitat requirements, but not about the environmental parameters that may be limiting the observed range of a given species. Broadly distributed species are more easily tested for association with various habitat parameters. Comparison of their abundance across micro-habitats over time or space may also be useful for identification of microclimate change.

Six species with a broad distribution over the *Weinmannia* host were chosen as potential microclimate change indicators. Each had a characteristic pattern of abundance (Table 23).

Table 23. Frequency in zone samples of six species with wide distribution on the *Weinmannia* sp.

	Zone					
Species	**1**	**2.1**	**2.2**	**3**	**4**	**5**
Lejeunea subgen. *Nanolejeunea* sp.	1	0.5	0.1	0.4	0.1	0.1
Macrolejeunea pallescens	1	1	0.8	0.7	0.8	0.2
Plagiochila stricta	0.8	1	0.5	0.7	0.1	
Omphalanthus filiformis	0.1	0.7	0.5	1	0.9	0.8
Frullanoides densifolia subsp. *densifolia*		0.3	0.1	1	1	0.8
Frullania riojaneirensis		0.1		0.3	0.4	1

Lejeunea subgen. *Nanolejeunea* sp. is likely to be a facultative epiphyte, predominantly growing on the lower trunk. *Macrolejeunea pallescens* is an obligate epiphyte, with highest frequency on the lower and upper trunk. *Plagiochila stricta* was most commonly found along the upper trunk, but not in the outer crown. *Omphalanthus filiformis* appears to prefer mid-crown conditions. *Frullanoides densifolia* subsp. *densifolia* had highest frequency in the mid and mid-outer crown, while *Frullania riojaneirensis* is a high light specialist that was most frequently found in the outer crown.

Frequency of *L*. subgen. *Nanolejeunea* was most strongly correlated with the relative humidity values and diameter. All other variables did not have significant correlations (Table 24). This species has demonstrated a preference for the lower trunk habitat and may require high humidity or long periods of leaf wetness.

The abundance pattern of *Macrolejeunea pallescens* was most strongly, but negatively correlated with VisSky and the radiation variable, particularly the diffuse below fraction of below crown radiation. This is not surprising as all these variables, including LAI have been shown to be highly correlated. VisSky is very highly correlated with DifBe (r = 0.995). It appears radiation intensity, and especially diffuse radiation, more than RH or temperature, may have a negative impact on *M. pallescens* abundance.

Table 24. Pearson's correlation coefficients for associations of frequency of selected bryophyte species and environmental parameters: height above ground, diameter of branches and trunk, temperature, proportion of visible sky, leaf area index and total below, direct below and diffuse below radiation recorded on a *Weinmannia* sp. host. All associations shown were significant (P < 0.05).

	Height	Dia	RH	Temp	VisSky	LAI	TotBe	DirBe	DifBe
L. subgen. *Nano*.		0.80	0.82						
M. pallescens					-0.87	0.82	-0.84	-0.81	-0.86
P. stricta				-0.84	-0.88	0.84	-0.88	-0.87	-0.88
O.filiformis	0.84	-0.88	-0.90						
F. densifolia	0.90	-0.89	-0.91	0.91		-0.86		0.80	
F. riojaneirensis	0.87	-0.84		0.82	0.96	-0.89	0.95	0.93	0.95

Radiation intensity was also strongly correlated with the frequency of *P. stricta*, but for this species, the negative relationship was nearly as strong with both the diffuse and direct fraction of below crown radiation. The frequency of *P. stricta* drops off quickly in the mid-crown, apparently affected by high irradiation and rising temperature, suggested by the high negative correlation to VisSky and temperature, which themselves were shown to only have a moderately strong association (Table 20). Curiously, this species was most frequently found on the sheltered side of the trunk and not on the less illuminated lower trunk, suggesting a narrow range of irradiation tolerance and a preference for moderate radiation intensity.

Frequency of *Omphlanthus filiformis* was most closely aligned with the relative humidity, but also with branch diameter and height above ground. The negative relationship with Dia and RH suggests a low tolerance for lower trunk sites where the humidity is high. Its high frequency in the upper crown indicates a tolerance of, if not a requirement for high radiation intensity.

The negative correlation of *F. densifolia* with Dia, RH and LAI reflects its highest frequency in the mid-outer crown. Its requirement for moderately high radiation intensity is suggested by the strong negative correlation with LAI and a positive relationship with DirBe. A reduction in frequency in the outer crown may indicate the prevalence of suboptimal light conditions (excessive radiation) or desiccation regimes in that section of the crown. Preferred position of *F. densifolia* and the high correlation with temperature may indicate a physiological requirement for temperatures higher than those found near the forest floor.

High radiation intensity was a possible requirement for *F. riojaneirensis*. Its frequency was most strongly correlated with VisSky and the radiation variables. The observed preference of this species for the twiggy outer crown is confirmed by the negative correlation with Dia (Table 24).

5.3 Discussion

The selected environmental variables were well correlated with each other, resulting in low dimensionality in the ordination space. Temperature had the weakest associations of any variable tested. Lee and La Roi (1979) found that bryophytes were much more sensitive to fluctuations in moisture than temperature. There was less than 0.5˚C difference in mean temperature between the coolest and warmest sections of the host. During the warmest part of the day, a little over 1˚C separated the sheltered side of the trunk, the coolest part of the *Weinmannia* and the highly irradiated upper crown. The small temperature gradient on this host may not directly have a significant impact on species physiology and distribution. However, the relative humidity gradient is co-dependent on temperature. The importance of relative humidity to spatial distribution of epiphytic species is discussed below.

5.3.1 Height

Height above the ground was most strongly correlated with the variation in species composition on the *Weinmannia* in the initial ordination. The strongest correlation along

the second axis was attained by the variable diameter with a score of just 0.149. The very low correlations along the secondary axis reflect the narrow spread of the environmental variable vectors and make any interpretation of the second axis impractical. The first PCA axis explained 87.64% of the variation in the environmental data was perhaps a good early indication of the strong alignment of environmental variable vectors with height above the ground.

Variation in species composition in a Venezuelan cloud forest was also best correlated with height above the ground (Kelly *et al.*, 2004). They found the horizontal gradient or change in the vegetation type to also to be important. The most closely correlated environmental variables in Wolf's study (1994) were altitude above sea level and height within the host tree. Catchpole (2004), in his study of vascular epiphytes on a nearby tree also identified the vertical gradient or zones within the tree, to be highly correlated with species distribution.

The most highly correlated environmental variable in the present study, height above the ground, eloquently summarises the environmental variation along a tree host. The vertical extension of the host is an inherent component of each environmental variable used in the present study. To put any of the variables or communities into context, it is necessary to refer to height above the ground. It is important to note that 'height' is a relative rather than an absolute concept in the context of epiphyte distribution on a tree host. The transition from the lower trunk to mid-crown to the outer crown follows similar gradients in a 20 m emergent host and a 40 m emergent, with similar impact on the community composition in various sections of a host (pers. obs.). When comparing epiphyte communities, it is important to refer to both height and section of the host. It appears that height is a 'nuisance' variable and does not provide any new information beyond widely recognised species stratification in tree hosts.

Radiation, and particularly diffuse radiation, was also very strongly correlated with species distribution in the initial ordination and remained so following the removal of the variable height in the second analysis. Various physiological studies have identified intensity and

quality of radiation as important to vertical distribution of epiphytes (Hosokawa *et al.*, 1964; Tobiessen *et al.*, 1977; Proctor, 1990). Majority of bryophytes in neotropical lowland forests are epiphytes (Gradstein, 1995); less than 1% of above crown radiation may reach the forest floor (Kira and Yoda, 1989). The level of light interception by the canopy in montane forests may be lower than beneath the closed and more uniform canopy of lowland rainforests, as shown by the present study. However, higher light availability closer to the forest floor in montane cloud forests promotes the growth of a dense understorey and similarly encourages bryophytes to adopt epiphytic habitats, either in the crown or on stems and branches in the understorey. Frequency of four of the six chosen indicator species were strongly correlated to radiation, either negatively, for species commonly inhabiting the lower sections of the host or positively, for species of the upper crown. Outer canopy sun epiphytes, like *Frullania brasiliensis*, descend to the understorey or forest gaps if there is sufficient light.

Solar radiation reaching the forest canopy is composed of the direct and diffuse fractions. The diffuse fraction of solar radiation, be it due to refraction caused by cloud or suspended dust particles, or shading by canopy foliage, is used more efficiently by plants than the direct component. Higher rates of photosynthesis have been related to an increasing ratio of diffuse to direct radiation (Goudriaan, 1977; Cu *et al.*, 2002). The magnitude of photosynthetic enhancement reported in literature varies from 2-3 times to 6-33% that obtained with conditions dominated by direct radiation (Gu *et al.*, 2002; Johnson and Smith, 2006; Alton *et al.*, 2007). However, there is a general consensus that under conditions dominated by diffuse light, PAR is less variable and photosaturation is less likely to occur, which leads to an overall increase in assimilation rates across a range of plant canopies. The benefits of higher levels of diffuse light are more pronounced at high radiation intensities (Gu *et al.*, 2002), that could be expected at high altitude in the tropics. Tropical cloud forests appear to provide close to ideal conditions for bryophytes; cool temperatures, high moisture availability and a favourable light environment.

5.3.2 Diameter

The parameter diameter was most strongly associated with the species distribution along the secondary axis in the second ordination, axis 1. Diameter, not unlike height, encompasses an array of gradients and may draw attention away from more ecologically relevant parameters. Diameter summarises the gradients of bark age, with inclusive characteristics of texture and exposure to colonisation opportunities (Barkman, 1958; Van Leerdam *et al.*, 1990) and the horizontal gradients of temperature and relative humidity that extend along branches from the crown centre to the periphery (Freiberg, 1997; Freiberg, 2001). There is insufficient data in the present study to examine the influence of these confounding factors, which could become the subjects of some future study.

Relative humidity had the next strongest correlation with species distribution along axis 1. León-Vargas *et al.* (2006) have shown that relative humidity is of lesser physiological importance for bryophytes than leaf wetness. At full turgor, the osmotic potential for many bryophytes is between -1.0 and -2.0 MPa, which corresponds to a relative humidity of 98.5-99.5%. At lower humidity, the loss cellular moisture reduced turgor. And at 25% cell relative water content or relative humidity of 95%, photosynthesis stops. Humidity at levels high enough to maintain photosynthesis (>98%) can only be maintained in the presence of liquid water.

Bryophytes get around the problem of desiccation not just with various institutive cell protection and rehydration activated cellular repair mechanisms (Oliver and Bewley, 1997; Oliver *et al.*, 2000; Oliver *et al.*, 2004), but also by storing a large amount of water externally (Proctor, 1990; Proctor, 2004). Extracellular water, stored in leaf folds, sacks and lobules, so common among the outer crown hepatics, can extend the duration of the physiologically active periods, interrupted by desiccation episodes, for long enough to reach or surpass the respiration compensation point. This is where relative humidity comes into play. The external water evaporates more slowly with greater vapour content in the atmosphere, leading to longer periods of assimilation. So, although relative humidity may not directly have a great impact on bryophytes, it does affect the duration of leaf wetness and the rate of desiccation, which have been linked to the tolerance of

desiccation by individual species and composition of epiphytic bryophyte communities in different parts of tree hosts (Proctor, 1981; Sillett *et al.*, 1995; León-Vargas *et al.*, 2006).

5.3.3 Why is the exposed side of the trunk so different?

The division of the mid and upper trunk into an exposed and sheltered side rather than a lower and an upper section, as is more customary, was encouraged by the visually apparent difference in the volume of epiphytes supported by each side. The differences in species composition and values of the environmental parameters between the two sides were hoped to assist identify the illusive environmental parameter driving the overall species distribution on the host. However, the collected data provided many contradictory clues.

Zone 2.2 had higher average VisSky and temperature, but lower LAI and RH than the sheltered side of the trunk, as was expected (Fig. 9A, Fig. 12). The values of environmental variables for the sites on the exposed side of the trunk generally fitted well into the gradients extending from the lower trunk to the outer crown. Diffuse radiation made up a larger proportion of total radiation received by zone 2.2, which could be explained by its south-westerly aspect (Fig. 14B). Inspection of hourly means for temperature and relative humidity in fine weather revealed greater temperature and RH fluctuations in zone 2.2, which was warmer during the day, but cooler at night than zone 2.1 (App. II). This agrees with Frieberg's (2001) findings for branches without a thick bryophyte cover. The higher night time relative humidity recorded on the exposed side of the trunk could be explained with the inverse relationship of temperature and relative humidity.

The poor correlation between species presence and values of environmental parameters was puzzling. The species found on the exposed side of the trunk were generally a reduced selection of those recovered from the sheltered side (Table 8). Some of the missing species were most frequently found in the mid and mid-outer crown, but were present on the sheltered side. Others had highest frequency on the lower trunk and also occurred in zone 3, but not on the exposed side of the trunk, which did not fit the observed

environmental gradients. Just two species, *Zygodon obtucifolius* and *Zygodon gracillimus* had their highest frequency in Zone 2.2. Both are tiny species with thick cell walls; a strong hint why zone 2.2 had such a poor bryophyte cover. *Z. gracillimus* was reported in montane forest at 2200 m in much drier Bolivia (von Malta, 1926). *Z. obtucifolius* is an obligate epiphyte found at high elevation or at harsh sites.

One piece of evidence that has not yet been highlighted is the slight lean of the trunk to the south. The combination of aspect and location on the underside of the leaning trunk appears to create a more heavily shaded, but most importantly, a drier habitat than indicated by the environmental data. Drizzle or light rain is likely to be predominantly captured by the epiphyte rich upper side of the trunk. Essentially, the exposed side of the trunk is analogous to the generally drier and less irradiated branch undersides, which frequently are bare or support a specialist community capable of survival in such demanding conditions (Norris, 1990).

5.4 Conclusion

It appears that radiation intensity, particularly the diffuse fraction of below radiation, and relative humidity may be the most influential environmental parameters on the composition of bryophyte communities on the *Weimannia* host. However, the lower trunk and outer crown communities represent two poles of a continuum of species tolerances and adaptations, evident from the overlapping species distribution and varied abundance. The importance of these two or any other environmental variables is likely to be interpreted differently by each species and the overall community composition may be strongly influenced by the microclimate of each host, itself influenced by tree architecture and its radiation interception characteristics. Nevertheless, radiation intensity and moisture availability have been identified by many earlier studies introduced above as important parameters limiting species distribution.

The visible sky proportion had a strong relationship with the radiation variables in the present study, and particularly with diffuse light fraction ($r = 0.995$, $R^2 = 0.991$, $P < 0.000$) and may be useful as a rough indicator of the more complex radiation parameters.

Chapter 6. Conclusion

Some of the discussion presented in this chapter relies on data amalgamated across the three sampled trees. Despite the contrasting methodology employed to sample the *Alchornea* sp. and *Croton* sp., and *Weinmannia* sp. hosts, some valuable conclusions can be drawn about epiphytic biodiversity patterns in lower montane rainforests. The present study provides important baseline information and novel data necessary for formation of conservation strategies of Peruvian bryophytes and montane forests in general.

6.1 Floristics and community structure

In total, 129 bryophytes in 19 moss and 18 hepatic families were found on three hosts (App. VI). The most species rich families among the mosses were Pilotrichaceae (3 genera/6 species) and Meteoriaceae (3/5). Orthotrichaceae was represented by just one genera, *Zygodon* and four species. Some of the other species rich genera included *Trachyxiphium* (3 spp.) and *Macromitrium* (3 spp.). Lejeuneaceae (23/39) was by far the most represented hepatic family, making up 30% of the epiphytic bryophyte flora. Other speciose families were Lepidoziaceae (3/4), Jubulaceae (2/7) and Geocalycaceae (2/6). Thirteen *Plagiochila* species were recorded; *Lejeunea* was the second most species rich genus with 6 species. Others included *Lophocolea* (4), *Drepanolejeunea* (4), *Metzgeria* (4) and *Cheilolejeunea* (3). Qualitatively similar findings were reported by other studies (Gradstein, 1995; Kürschner and Parolly, 1998; Nöske *et al.*, 2003) and agree with the earlier found floristic similarity at the genus level, across broad areas of the Neotropics (Gradstein, 1995; Gradstein *et al.*, 2001a).

Eighty-eight hepatic species (including 1 hornwort) and 41 mosses were collected. The overall hepatic to moss ratio for the three trees was 2.15:1 (Fig. 38). The lower altitudinal range and greater turnover of mosses than hepatics above 2130 m have led Wolf (1993a) to conclude that mosses may generally have narrower tolerance ranges than hepatics; an opinion also shared by Florschutz-de Waard and Bekker (1987). The present study offers data in support of this hypothesis. Hepatics had a higher turnover of species than mosses along the upper trunk, but lower in other sections of the *Weinmannia* host (Table 11).

Fifteen bryophyte species were found throughout the hosts, but just two were mosses, *Daltonia longifolia* and *Zygodon reinwardtii*, while the majority of mosses were more limited in their distribution. All of the outer crown faithful species found on the *Weinmannia* host were hepatics, but 42% of species only found in the mid to mid-outer crown were mosses. The proportion of microhabitat faithful moss species reduced to 25% on the upper trunk and 27% on the lower trunk, indicating a clear preference for the moderate conditions of the mid-crown.

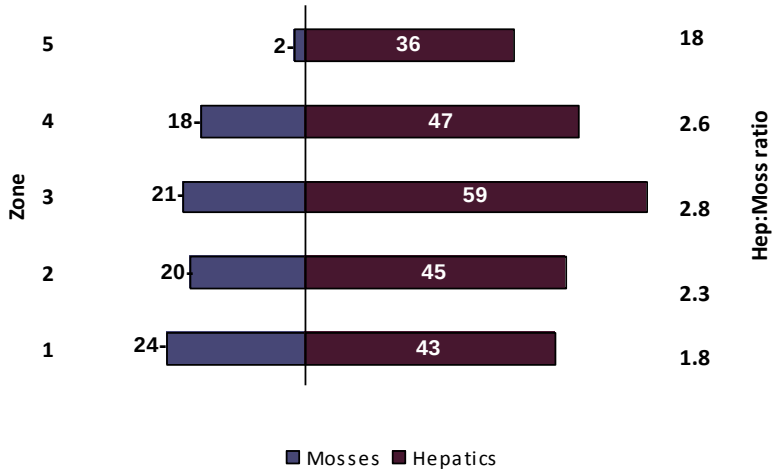


Fig. 38 The number of hepatics and mosses found on 3 tree hosts. Sampling was stratified by Johansson (1974) zones. The hepatic to moss ratio in each zone is indicated on the right.

The proportion of obligate epiphyte species in each zone rose with height above the ground (Fig. 39). Just two moss species were found in the outer crown, both were obligate epiphytes. The outer crown was dominated by hepatics, predominantly by pendulous mats of *Frullania riojaneirensis*, but also supported a rich flora of exclusive species like *F. stenostipa*, *Diplasiolejeunea* sp., *Colura tenuicornis* and *Aureolejeunea fluva* (Fig. 26, 33). Fruticose lichens were abundant. Similar observations were made in the tops of cloud forest canopies by other studies and related to frequent wetting (Wolf, 1993c; Kelly *et al.*, 2004). The outer crown community (Table 15) was perhaps the most distinct of the assemblages found on the *Weinmannia* host and was clearly separated by both classification and ordination. The *Frullania stenostipa-Lejeuneaceae* sp. 2 community of

the outer crown described in the present study is similar to the *Diplasiolejeunea pauckertii-Brachiolejeunea laxifolia* community in Colombia described by Wolf (1993b).

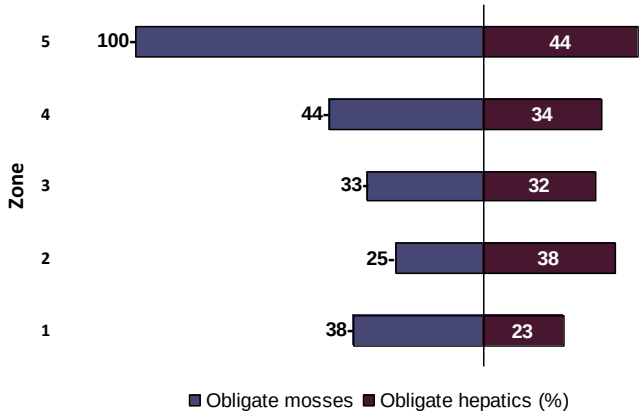


Fig. 39 Contribution of obligate species to the overall zone (Johansson, 1974) moss and hepatic species richness. Species presence was sampled with different methodologies on three tree hosts at 2400 m in lower montane rainforest, Peru.

The bryophyte community in the mid-outer and mid crown of the *Weinmannia* was dominated by broadly distributed species, reflecting the middle of the gradients of irradiation, temperature and relative humidity extending from the ground to the crown periphery. This finding contrast with that of Wolf (1974) and Sillett *et al.* (1995) who report most restricted ranges for species in the mid-crown, but concurs with species distribution patterns found on an ancient *Lagarostrobos franklinii* in cool temperate rainforest (Jarman and Kantvilas, 1995a). The *Frullania densifolia*, *Omphalanthus filiformis* and *Macromitrium aureum* dominated community in the present study was also rich in exclusive taxa that included *Leptoscyphus porphyrius*, *Squamidium livens* and *Mnioloma cyclostipa* among others (Table 16). The *L. porphyrius–M. aureum* community of the mid-crown shares a number of key taxa with the *Omphalanthus filiformis* community described by Wolf (1993c). The branches were thickly covered with interwoven mats of bryophytes (Fig. 24); thirty-five species were found in just one square decimeter sample on the *Alchornea* sp.

There was a large overlap of species between the assemblages found on the upper trunks and both the mid-crown and lower trunk sections. The trunks supported the least number of exclusive taxa (Table 17) and the frequency of presence of many species indicated that the trunk is a transition zone. Many crown species had their lowest distribution along the upper trunk, which was also the highest extension of some lower trunk specialists (Table 8). The trunks had a lower hepatic to moss ratio than the mid-crown, suggesting the prevalence of more xeric conditions. Apart from the trunk exclusive species, only 2 more widely distributed species had their highest distribution on the trunk. Both were hardy *Zygodon* sp.

Interestingly, the lower trunks, often a domain of lowlight and moisture loving hepatics had a relatively high species representation of mosses (Fig. 38). This finding is puzzling as the lower trunk was the most humid and least irradiated of habitats sampled. The lower trunk supported the highest number of facultative epiphytes (Fig. 39). The *Riccardia smaragdina-Rhizogonium novae-hollandiae* community (Table 18) described in the present study was similar to the *Mittenothamnium reptans* lower trunk community described by Wolf (1993c), illustrating the generally wider distribution of bryophyte species than has been found for the neotropical vascular flora (Gentry, 1992a; Gradstein, 1995).

The proportion of crown or trunk exclusive species is informative about the forest structure and associated availability of light on the forest floor. Cornelissen and Gradstein (1990) found that in Guyana lowland rainforests about 50% of the bryophytes were restricted to the crowns, that is more than 10 m above the ground and 14% to the understorey. A later study in Monteverde cloud forest, Costa Rica revealed a similar crown proportion, 52%, with 20% restricted to the understorey and 28% of species shared both habitats (Gradstein *et al.*, 2001b). The proportion of crown exclusive species in the present study (zones 3-5), was lower. Thirty one percent of species collected were only found in the crown, 22% were limited to the trunk. The majority, 47% had wider distributions, either throughout the hosts or over sections of the trunk and crown (Fig. 40). The lower proportion of crown exclusive and higher number of broadly occurring species

found in the present study suggest that light interception by the canopy at the El Cedro study site may be lower than at the lowland and Costa Rican montane rainforest sites. A mean of 3.8% of the sky was visible in zone 1 of the Weinmannia host and 14.6 % in zone 3.

6.2 Species richness and sampling methodology

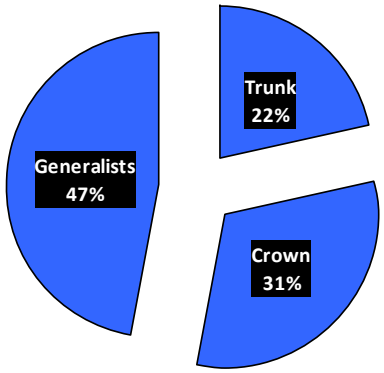
The low intensity sampling effort employed in the pilot study yielded only 81 and 65 species on the *Alchornea* sp. and *Croton* sp. hosts respectively, compared to 110 species found on the *Weinmannia* host with much more intensive sampling. The total sample area in the pilot study was approximately 0.3 m^2. This was equivalent to ten subsamples collected on the *Weinmannia* or 60% of the total species richness for that host. If similar sampling intensity were applied to the *Alchornea* and *Croton* trees, the total species richness for these hosts, based on observed species numbers, is estimated at 135 and 108 species respectively, numbers comparable to the 110 species recovered from the *Weinmannia*. Nineteen species collected during the pilot study were not seen on the *Weinmannia* and a conservative estimate of the overall species richness for the three hosts is 141 species.

Many studies of epiphytic bryophytes have adopted the 75% species capture rate as a stopping rule or a gauge of adequate sampling effort (Wolf, 1993b; Gradstein *et al.*, 2001b; Gradstein *et al.*, 2003a). The pilot study demonstrated that a subsample of 0.03 m^2 is adequate to capture at least 75% of species richness in a sample double that size (Table 2 and 3). Seventy five percent of the observed species on the *Weinmannia* were recovered in just eighteen 0.03 m^2 samples (the present study sampled a 300 mm length of branch in the mid-outer and outer crown as equivalent to a 0.03 m^2 subsample). The mean predicted species richness for the host was 120 or 8% higher than the observed species number (Fig. 27). After adjustment for the missed species, the minimum sample size (> 75% species capture) for epiphytic bryophytes in lower montane rainforest on the Yanachaga Range should be no less than 0.6 m^2 or 20 samples (0.03 m^2 each) located throughout a tree host.

Trunk
Mosses
Fissidens serratus
Holomitrium arboreum
Rhizogonium novae-hollandiae
Sematophyllum galipense

Hepatics
Cephaloziella granatensis
Jubula pensylvanica subsp. *bogotensis*
Lepidozia caespitosa
Leptolejeunea elliptica
Lophocolea muricata
Monoclea gottschei
Plagiochila harrisana
Riccardia smaragdina
Trichocholea flaccida

Generalists
Mosses
Daltonia longifolia
Zygodon reinwardtii
Hepatics
Dendroceros crispus
Drepanolejeunea infundibulata
Frullania riojaneirensis
Lepidolejeunea eluta
Macrolejeunea pallescens
Metzgeria decipiens
Omphalanthus filiformis
Plagiochila bifaria



Crown
Mosses
Brachymenium consimile
Macromitrium longifolium
Macromitrium podocarpi
Meteorium illecebrum
Squamidium livens
Trachyxiphium variable
Hepatics
Aneura pinguis
Anopolejeunea conferta
Aureolejeunea fluva
Ceratolejeunea maritima
Chielolejeunea subgen. *Strepsilejeunea* sp.
Colura tenuicornis
Diplasiolejeunea sp.
Drepanolejeunea araucariae var. *araucariae*
Frullania stenostipa
Leptoscyphus physocalyx
Leptoscyphus porphyrius
Lophocolea trapezoidea
Mnioloma cyclostipa
Squamidium leucotrichum
Streptopogon calymperes
Syrrhopodon graminicola

Fig. 40 Crown limited (zones 3-5), trunk limited (zones 1-2) and generalist species as a proportion of the total species richness recorded on 3 tree host. The generalist species list includes only species present in all zones and on all hosts.

The protocol for rapid and representative sampling offered by Gradstein *et al.* (2003) advise collection of five samples of 0.06 m^2 from zones 1-3 and a epiphytes from five 600

mm long sections of branch in zone 4-5. Based on the findings of the present study, this method should yield more than 75% species capture, at least in a habitat similar to that of the present study. The time required to process each sample is considerable and each project needs to balance the available resources with the aims and scope of the study. Microhabitat diversity on each host also needs to be considered and a choice made whether to put more emphasis on species capture or statistical correctness (see introduction to Chapter 2). The pilot study findings hinted at an existence of a relationship between species density and species capture. A single sampling method applied across habitats of varying species richness may produce negatively biased results for habitats with low species density, exaggerating the contrast between species rich and the less rich habitats. It appears that the difficulties in comparing different studies or forest types, like the species rich upper montane rainforests with less bryophyte rich lowland rainforest, will not be completely resolved simply by applying a uniform sampling method. More detailed studies are needed to evaluate bryophyte species capture rates across habitats with different species density.

6.3 Microclimate and other environmental parameters

6.3.1 Microclimate

The microclimatic fluctuations recorded on the *Weinmania* sp. generally agree with findings of other studies conducted predominantly in lowland forests (Freiberg, 1997; Szarzynski and Anhuf, 2001). One contrasting report is that of Catchpole (2004) conducted at a nearby site on the Yanachaga-Chemillén Range, which highlights the heterogeneity of the montane forest canopy and the strong influence crown architecture and permeability can have on the microclimate and the epiphyte population it supports.

Opposing gradient of temperature, humidity and radiation intensity existed between the lower trunk and the outer-crown periphery of the *Weinmannia* host. Mean lowest temperature and highest humidity occurred near the ground. The lowest proportion of visible sky, highest leaf area index and lowest photosynthetically active radiation intensity was also recorded on the lower trunk. The microclimate in the outer crown was most

varied, while the diurnal range of temperature and relative humidity near the ground was smaller than in any other microhabitat on the *Weinmannia*.

The diurnal fluctuations of temperature and relative humidity throughout the *Weinmannia* were affected by the prevailing macroclimatic conditions. Wet and cloudy weather compressed the otherwise clear gradients between the lower trunk and the crown periphery. Mean hourly values revealed a complex interaction of temperature, relative humidity and radiation, influenced by the structure of the host (Fig. 16). Highest day temperatures were recorded between 1 and 3 pm in the highly irradiated mid-outer crown, just 0.03˚C warmer than the crown periphery. The slightly higher temperature in zone 4 than in zone 5 may have been the result of lower wind speeds and greater surface area and mass of the branches lower in the canopy. The air above the crown at the warmest time of the day was 0.48˚C cooler. Lowest daytime temperature was recorded along the upper trunk. Decoupling of the crown from the atmosphere closer to the ground induced by higher radiation interception and warming of the crown did not appear as pronounced as observed in lowland forest, possibly due to greater mixing of the below canopy atmosphere facilitated by the more open canopy characteristic of montane forests on steep slopes. However, the gradient of relative humidity remained strong and an average of 14% difference separated the lower trunk and the upper crown by the middle of the day. The average temperature difference between the same sections of the host was 1.1˚C at 3 pm. The profile begun to cool after 4 pm. Radiative cooling in the outer to mid crown forced a reversal of the temperature gradient and the coolest night temperature was recorded in the mid-crown at 6 am. The air above the crown had a higher night temperature than any habitat on the Weinmannia. As the sun warmed the crown in the early morning, the temperature and relative humidity gradients re-established the daytime pattern.

A different pattern of diurnal fluctuation was found on a *Ficus* sp. by Cathchpole (2004). Lowest temperature occurred near the ground and above the crown. During the day, the mid-crown was cooler than the above crown temperature. The contrasting tree architecture, canopy density and epiphytic community combined to create a starkly

different crown microclimate to that found in the present study. Difference in canopy structure was suggested as a possible cause of variation in epiphytic bryophyte composition between two types of temperate montane rainforest in Tasmania (Dalton, 1998). The heterogeneous canopy of montane forests appears to provide a rich array of microclimates, reflected by the exceptional diversity of both vascular and non-vascular flora in the tropical Andes.

6.3.2 Environmental parameters

Height above the ground and diameter had the strongest correlations with the first two ordination axes of species and environmental variable data recorded on the *Weinmannia* host. Both of these variables are inherent components of all environmental gradients measured. Height above the ground is an essential reference when describing temperature, relative humidity, light interception and radiation intensity throughout a tree host. Diameter was strongly correlated with height above the ground and itself summates a host of gradients like bark age, exposure to colonisation opportunities (Van Leerdam *et al.*, 1990) and perhaps most importantly, the horizontal gradient of temperature and humidity extending from the crown centre to the periphery (Freiberg, 1996), unfortunately not measures in the present study. The strong correlation of height above the ground or the related host Johansson (1974) zone with species data has also been reported by other studies of epiphytic bryophytes (Wolf, 1994; Catchpole, 2004; Kelly *et al.*, 2004). However, like diameter, it does not offer any new information beyond confirming already accepted variation of epiphytic community composition with distance from the ground and canopy centre. It is proposed here that height above the ground and diameter are 'nuisance' variables and their continued interpretation as important for the distribution epiphytic flora detracts from more meaningful parameters.

Below crown diffuse radiation and relative humidity were the second most strongly correlated variables to the ordination axes. Light is a basic requirement for autotrophic organisms and its quantity and quality has been identified in ecophysiological studies to influence growth and preferred location of epiphytic bryophytes along the declining gradient from the outer crown to the lower trunk (Hosokawa *et al.*, 1964; Tobiessen *et al.*,

1977; Proctor, 1981). Relative humidity may have limited direct impact on the physiology of epiphytic bryophytes (León-Vargas *et al.*, 2006), but it does influence the duration of leaf wetness and consequently, the duration of active photosynthesis by bryophytes between periods of desiccation. Distribution of bryophyte species along moisture gradients has been suggested by other research (Barkman, 1958, Hosokawa *et al.*, 1964; Tobiessen *et al.*, 1977; Proctor, 1981; Sillett *et al*., 1995; Jarman and Kantvilas, 1995).

6.4 Future research needs

Montane rainforests in the Andes are under growing pressure from the expanding human population and related agricultural and forestry activities (Young, 1992b). The expected rise in the cloud base over the tropics as a consequence of global warming, also has the potential to dramatically change the ecology of montane forest and especially cloud forests (Benzing, 1998). Besides their intrinsic value, cloud forests are valuable sources of water, stripped from passing clouds by tree crowns and epiphytic vegetation. Horizontal precipitation in montane cloud forests can augment dry season precipitation by between 9 and 85% (Bruijnzeel and Proctor, 1995a). Bryophytes are an important component of cloud forest epiphytic flora and have been shown to be efficient captors of fog, enhancing not just the stream flow, but also the availability of essential nutrients like inorganic nitrogen (NO^-_3) captured from wet deposits (Clark *et al.*, 1998; Burns, 2003; Chang *et al.*, 2006; Luo *et al.*, 2007). Little is known about the cloud stripping potential of epiphytic flora, including bryophytes, and its contribution to net precipitation in Andean montane forests. This is a challenging area of research, but the resulting information would contribute to the formulation of water management and conservation strategies and possibly enhance the awareness of the local population of the value of cloud forests.

Six bryophytes species were identified as potential microclimate change indicators (Table 23) in hope of seeding future research that would facilitate the employment of this highly sensitive group of plants for early identification of changes in forest climate at the habitat level. Much more replication is necessary than was possible during the present study to evaluate the utility of the selected species and to map their distribution along an elevation gradient.

Despite the apparent environmental services provided by bryophytes, they remain undervalued and poorly known in the Neotropics. New records continue to be reported. A recent survey of the Reserva Biológica San Francisco in Southern Ecuador resulted in 63 new records for that country, most of those hepatics (Nöske *et al.*, 2003). Even in Monteverde, Costa Rica, perhaps the best studies cloud forest in the Neotropics, 19 previously unreported species were found in 2001 (Gradstein *et al.*, 2001b). The present study proposes 27 species, 5 mosses and 22 hepatics as new to Peru. A large proportion of bryophyte diversity in tropical rainforests remains hidden in the canopy. It is likely that the current estimates of species richness in rainforests, and particularly montane cloud forests are very conservative. Further taxonomic surveys and related studies, like the evaluation of species capture rate across habitats with different species density suggested earlier, are urgently needed to record the richness of the Andean bryophyte flora, but also to raise the awareness of the local population of the treasure lying at their doorstep.

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Appendix I Taxonomic literature used in species identification (by genus).

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Lejeunea subgen. Nanolejeunea

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Grolle, R. 1987. Zur Kenntnis der Lejeuneoideae in Cuba (2): *Lejeunea* subgen. *Macrolejeunea* Spruce. Mathematisch-Naturwissenschaftliche Reihe, **37**, 169-176

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To check for var illecebrum

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Prionodon
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Radula
Yamada, K. 1987. *Radula*. In W. Schultze-Motel & M. Menzel. Die Lebermoosflora im BRYOTROP-Transect von Peru. Beihefte zur *Nova Hedwigia*, **88**, 77-81

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Bischler, H. 1968. Monographie de genere Rhaphidiolejeunea Herzog. *Revue Briologique et Lichenologique*, **36**, 56-104.

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Scapania
Hong, W. S. 1988. Studies on *Scapania portoricensis* Hampe & Gott. in Latin America. Lindbergia, **14,** 69-72.

Sematophyllum
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Squamidium
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Buck, W. R. 1987. Trachyxiphium subfalcatum (Hampe). *Brittonia*, **39**, 220
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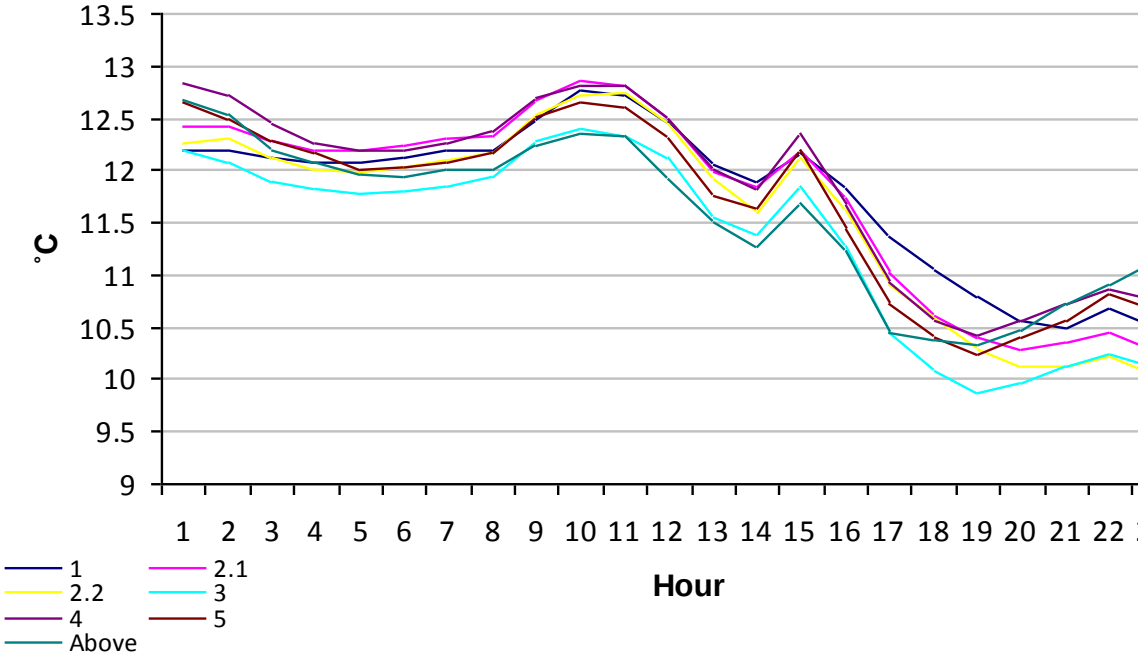
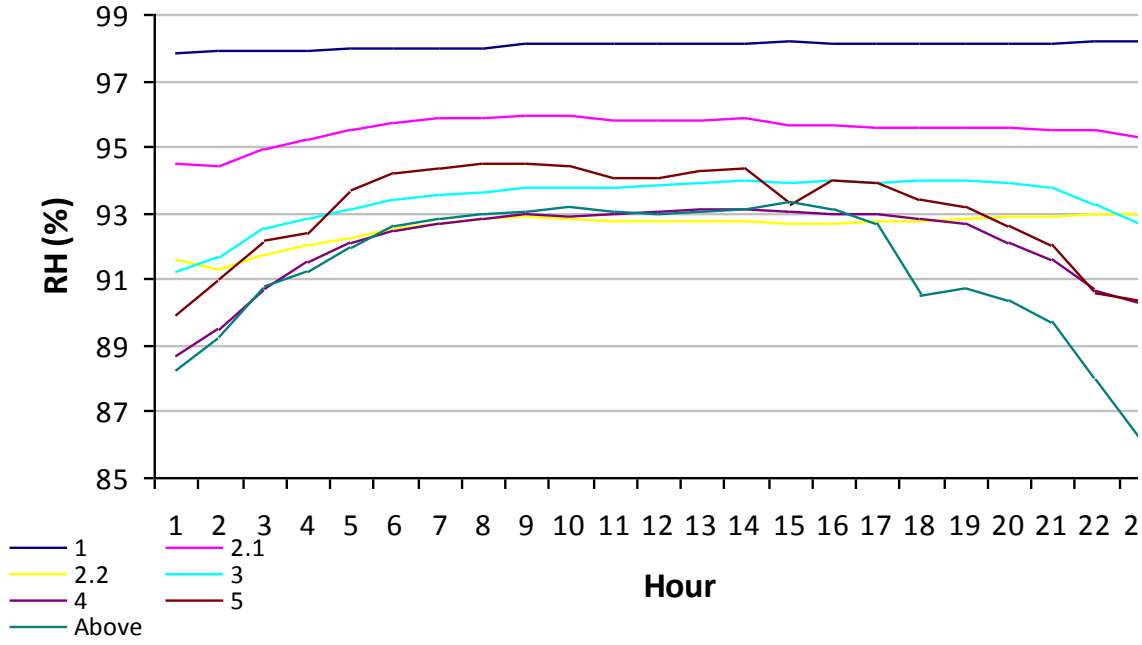
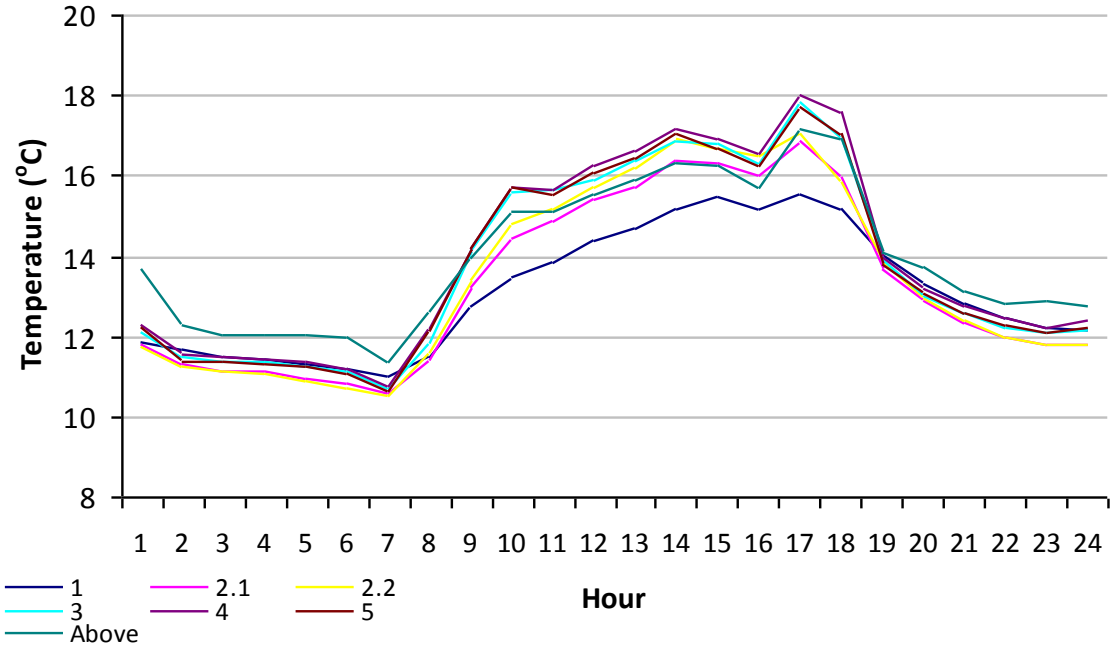
Appendix II Hourly wet and dry day temperature and humidity fluctuations.

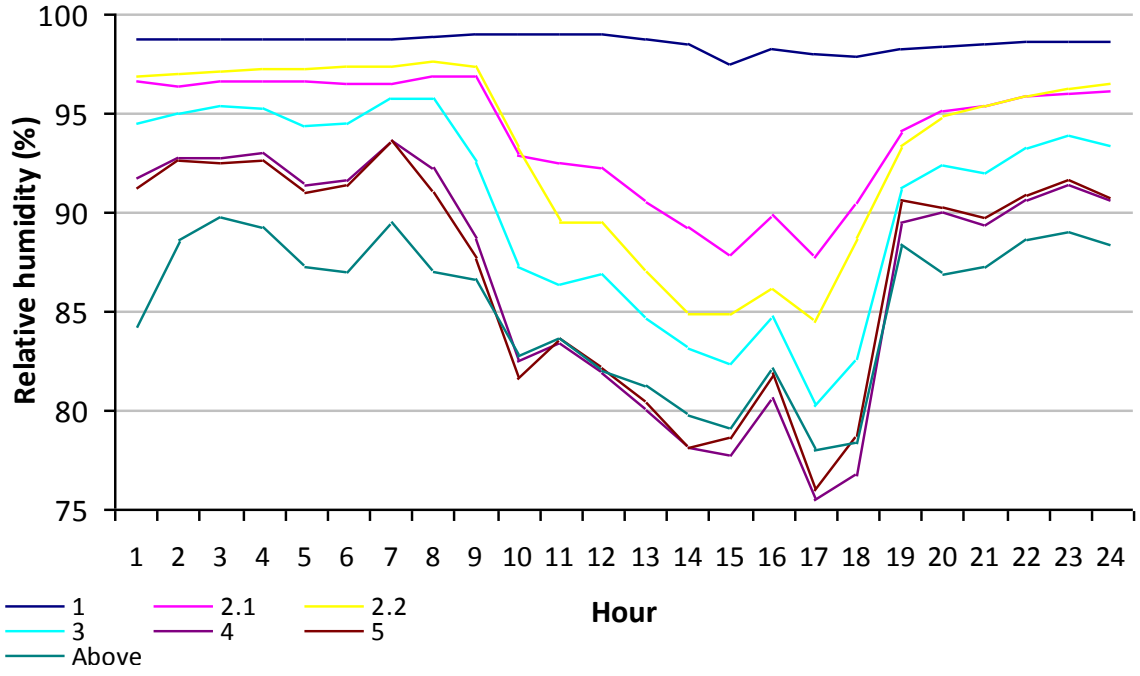
Hourly temperature and relative humidity during a rainy day, 21/10/2006.





Hourly temperature and relative humidity during a dry, sunny day, 14/11/2006.





Appendix III Bryophyte species found on the *Weinmannia* sp. host.

The proportion of samples in each Johansson zone (1974) where species were found (frequency) is shown in the columns on the right.
* - not previously recorded for Peru

Family	Name	Zone 5	4	3	2.2	2.1	1
Mosses							
Bartamiaceae	*Leiomela bartramioides*			0.1		0.5	0.3
Bryaceae	*Brachymenium consimile*		0.1				
Calymperaceae	*Syrrhopodon graminicola* *			0.1			
Daltoniaceae	*Daltonia longifolia*	0.3	0.1	0.1		0.1	0.1
Dicranaceae	*Holomitrium arboreum*						0.1
Fissidentaceae	*Fissidens serratus*						0.2
Hypnaceae	*Mittenothamnium reptans*		0.1	0.1	0.2	0.5	0.3
Hypopterigiaceae	*Hypopterigium tamarisci*					0.4	0.6
Macromitriaceae	*Macromitrium aureum*		0.9	0.7		0.2	
	Macromitrium longifolium		0.1				
	Macromitrium podocarpi		0.3				
Meteoriaceae	*Meteorium illecebrum*		0.2	0.1			
	Meteorium remotifolium		0.2	0.7	0.3	0.8	0.1
	Papillaria imponderosa		0.2	0.5		0.1	
	Squamidium leucotrichum		0.1				
	Squamidium livens		0.4	0.1			
Mniaceae	*Plagiomnium rhynchophorum*					0.2	0.6
Orthotricaceae	*Zygodon gracillimus* *			0.1	0.4	0.1	
	Zygodon obtusifolius			0.1	0.2	0.1	
	Zygodon reinwardtii	0.1	0.4	0.5	0.4	0.5	
Pilotrichaceae	*Lepidopilum caviusculum* *		0.1		0.1	0.2	0.5
	Lepidopilum scabrisetum			0.1		0.1	
	Trachyxiphium subfalcatum			0.1			0.2
	Trachyxiphium variable			0.1			
Pottiaceae	*Streptopogon calymperes*		0.1	0.1			
	Trichostomum brachydontium			0.3	0.1	0.2	
Prionodontaceae	*Prionodon densus*		0.3	0.5	0.8	0.8	0.1
Rhizogoniaceae	*Rhizogonium novae-hollandiae*						0.5
Sematophyllaceae	*Sematophyllum galipense*				0.1	0.1	
Thamnobryaceae	*Porotrichum longirostre*		0.4	0.7	0.4	1	1
	Porotrichum substriatum			0.1	0.1		0.2
Thuideaceae	*Thuidium peruvianum*				0.1	0.4	0.1
Hepatics							
Acrobolbaceae	*Acrobolbus antillanus*			0.1		0.1	
Aneuraceae	*Aneura pinguis*		0.1	0.2			
	Riccardia metzgeriaeformis		0.2	0.1		0.1	
	Riccardia smaragdina *						0.6
Anthocerotae	*Dendroceros crispus*	0.1	0.1	0.2			
Calypogeiaceae	*Mnioloma cyclostipa*		0.1				
Cephaloziellaceae	*Cephaloziella granatensis*					0.1	

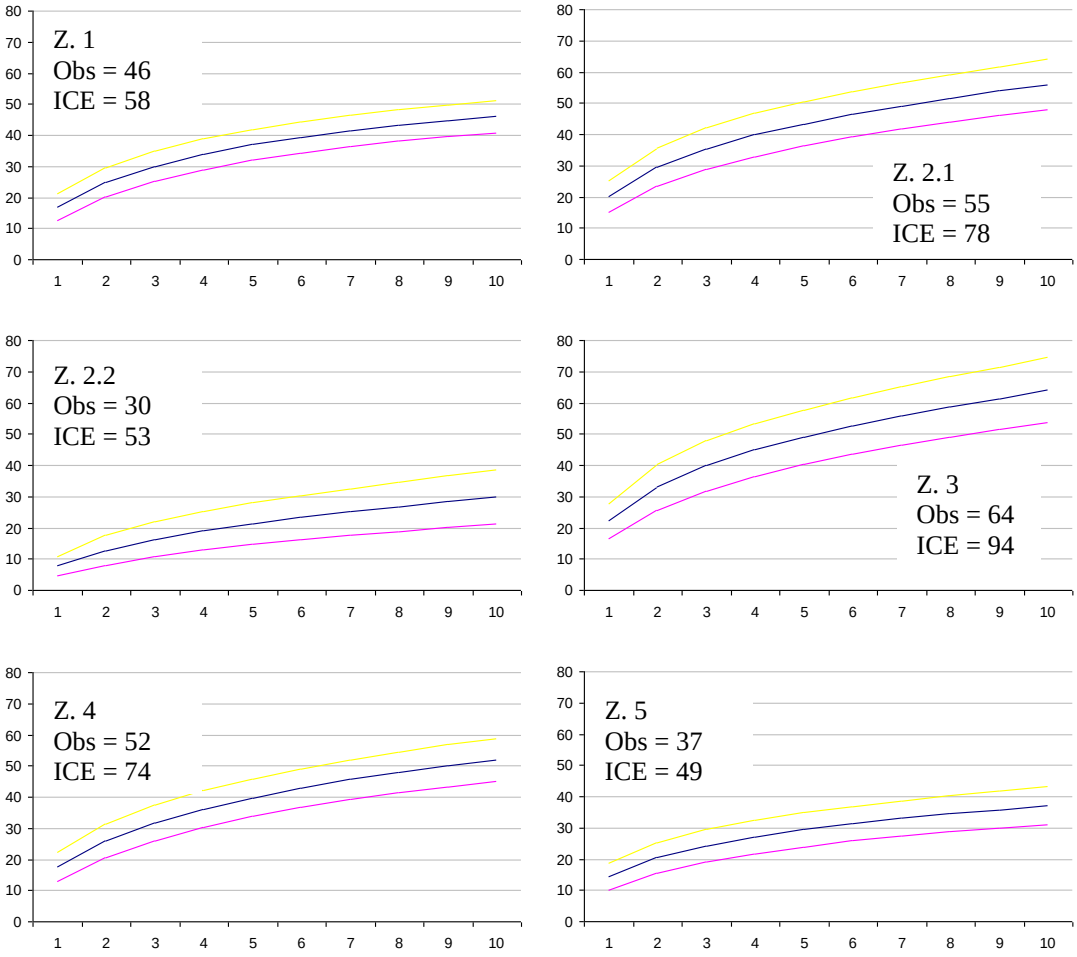
Family	Name	Zone 5	4	3	2.2	2.1	1
Hepatics cont.							
Geocalycaceae	*Leptoscyphus physocalyx*		0.2				
	Leptoscyphus porphyrius		0.3	0.5			
	Lophocolea coadunata			0.1			0.8
	Lophocolea muricata						0.4
	Lophocolea sp.			0.1			0.7
	Lophocolea trapezoidea			0.1			
Jubulaceae	*Frullania apiculata* *	0.3		0.1			
	Frullania brasiliensis *	0.9	1	0.9		0.5	
	Frullania riojaneirensis	1	0.4	0.3		0.1	
	Frullania sp. 5	0.4					
	Frullania stenostipa *	0.7					
	Frullania subgen. *Frullania* sp. 1	0.1	0.1	0.1			
	Jubula pensylvanica subsp. *bogotensis* *						0.4
Lejeuneaceae	*Lejeuneacea* sp. 2	0.8					
Lejeuneaceae (Tribe Brachiolejeuneae)	*Brachiolejeunea leiboldiana* *		0.1				0.1
	Brachiolejeunea spruceana *	0.8	0.1				
	Dicranolejeunea axillaris *		0.1	0.3	0.4	0.6	0.3
	Neurolejeunea breutelii *		0.5	0.9	0.1	0.3	
	Odontolejeunea lunulata	0.1				0.1	
Lejeuneaceae (Tribe Cololejeuneae)	*Colura tenuicornis*	0.1					
	Diplasiolejeunea sp.	0.4					
Lejeuneaceae (Tribe Lejeuneaceae)	*Amphilejeunea reflexistipula* *	0.1	0.1				
	Anopolejeunea conferta	0.2					
	Aureolejeunea fluva *	0.3					
	Ceratolejeunea deciscens *	0.3					0.1
	Ceratolejeunea maritima *			0.3			
	Cheilolejeunea comans *	0.5	1	0.7	0.1	0.6	
	Chielolejeunea subgen. *Strepsilejeunea* sp. 2	0.3					
	Drepanolejeunea araucariae var. *araucariae*	0.1					
	Drepanolejeunea infundibulata *	0.8	0.7	0.6	0.1	0.2	
	Harpalejeunea sp.	1	0.2	0.5		0.6	
	Lejeunea sp. 2			0.1			0.2
	Lejeunea sp. 3		0.2	0.2			
	Lejeunea subgen. *Lejeunea* sp. 1	0.2	0.7	0.2	0.1	0.2	0.3
	Lejeunea subgen. *Lejeunea* sp. *2*	0.2		0.6	0.5	0.8	0.1
	Lejeunea subgen. *Lejeunea* sp. 3	0.1					
	Lejeunea subgen. *Nanolejeunea* sp.	0.1	0.1	0.4	0.1	0.5	1
	Lejeuneacea Tribe *Lejeuneae* sp. 1		0.1	0.1	0.4	0.7	0.6
	Lepidolejeunea eluta	0.1	0.5	0.7	0.1	0.5	
	Lepidolejeunea spongia			0.1		0.1	
	Leptolejeunea elliptica					0.2	
	Macrolejeunea pallescens	0.2	0.8	0.7	0.8	1	1
	Macrolejeunea pallescens fo. *lancifolia*	0.7				0.1	
	Microlejeunea colombiana	0.5		0.1			
	Omphalanthus filiformis	0.8	0.9	1	0.5	0.7	0.1
	Oryzolejeunea sp. (ad aff *O. venezuelana*) *	0.5	0.7	0.3			
	Prionolejeunea decora *					0.4	0.4
	Prionolejeunea equitexta *					0.1	0.2
	Taxilejeunea pterigonia		0.2	0.8	0.1	0.7	0.4

Family	Name	Zone 5	4	3	2.2	2.1	1
Hepatics cont.							
Lejeuneaceae (Ptychantheae)	*Frullanoides densifolia* subsp. *densifolia*	0.8	1	1	0.1	0.3	
Lepidoziaceae	*Lepidozia caespitosa*						0.1
Metzgeriaceae	*Metzgeria decipiens*	0.1	0.2	0.4		0.7	0.7
	Metzgeria leptoneura					0.2	0.2
Monocleaeceae	*Monoclea gottschei*						0.1
Pallaviciniaceae	*Pallavicinia lyellii*			0.1			0.4
Plagiochilaceae	*Plagiochila aerea* *					0.1	0.1
	Plagiochila bifaria	0.2	0.8	0.6		0.1	0.1
	Plagiochila harrisana						0.3
	Plagiochila sp. 1	0.1	0.2	0.4	0.4	0.3	
	Plagiochila sp. 2		0.4	0.2			
	Plagiochila sp. 3		0.3	0.6	0.1	0.5	
	Plagiochila sp. 4			0.2			
	Plagiochila sp. 5		0.4	0.3			
	Plagiochila sp. 6			0.1		0.1	
	Plagiochila sp. 7				0.1	0.1	0.2
	Plagiochila sp. 8						0.2
	Plagiochila sp. 9					0.1	
	Plagiochila stricta		0.1	0.7	0.5	1	0.8
Radulaceae	*Radula montana*		0.8	0.7	0.1	0.8	1
Trichocoleaceae	*Trichocholea filicaulis* *		0.1	0.3		0.1	
	Trichocholea flaccida						0.2
	Mosses	2	16	20	12	18	15
	Hepatics	35	36	44	18	37	31
	110 species Zone totals:	37	52	64	30	55	46

* - not recorded for Peru

Appendix IV Species area curves for *Weinmannia* zones.

Blue - Observes species, Pink – 95% lower CI, Yellow – 95% upper CI



Appendix V Species code numbers used in classification and ordination plots.

No	Species	No	Species
1	*Plagiochila stricta*	61	*Dicranolejeunea axillaris*
2	*Zygodon reinwardtii*	61a(138)	*Aureolejeunea fluva*
2a	*Zygodon obtusifolius*	62	*Oryzolejeunea* sp. (ad aff *O. venezuelana*)
3	*Omphalanthus filiformis*	62a	*Lejeuneacea* sp. 2
6	*Lophocolea* sp.	63	*Meteorium remotifolium*
6b	*Lophocolea trapezoidea*	64	*Leptoscyphus porphyrius*
8	*Lejeuneacea* Tribe *Lejeuneae* sp. 1	64a	*Leptoscyphus physocalyx*
9	*Lejeunea* subgen. *Lejeunea* sp. 1	65	*Plagiochila* sp. 6
10	*Porotrichum longirostre*	65.1	*Cephaloziella granatensis*
10a	*Porotrichum substriatum*	68	*Cheilolejeunea comans*
11	*Trichocholea filicaulis*	68	*Chielolejeunea* subgen. *Strepsilejeunea* sp. 2
12	*Trichostomum brachydontium*	69	*Frullanoides densifolia* subsp. *densifolia*
13	*Macrolejeunea pallescens*	71	*Macromitrium aureum*
13b	*Macrolejeunea pallescens* fo. *lancifolia*	71c	*Macromitrium podocarpi*
14	*Drepanolejeunea araucariae* var. *araucariae*	71(97)	*Macromitrium longifolium*
15	*Thuidium peruvianum*	72	*Lepidolejeunea spongia*
16	*Radula montana*	74	*Jubula pensylvanica* subsp. *bogotensis*
17	*Lepidopilum scabrisetum*	79	*Holomitrium arboreum*
17(58a)	*Lepidopilum caviusculum*	81	*Odontolejeunea lunulata*
18	*Lejeunea* subgen. *Lejeunea* sp. *2*	83	*Lepidozia caespitosa*
18a	*Lejeunea* subgen. *Lejeunea* sp. 3	84	*Plagiochila* sp. 4
20	*Lejeunea* subgen. *Nanolejeunea* sp.	88	*Hypopterigium tamarisci*
21	*Daltonia longifolia*	92	*Acrobolbus antillanus*
21a	*Brachymenium consimile*	93	*Squamidium livens*
23	*Mnioloma cyclostipa*	93(133)	*Squamidium leucotrichum*
26	*Lejeunea* sp. 2	94	*Plagiochila* sp. 5
28	*Mittenothamnium reptans*	95	*Monoclea gottschei*
28a	*Sematophyllum galipense*	96	*Frullania riojaneirensis*
30	*Lophocolea muricata*	96(74)	*Frullania stenostipa*
31	*Prionolejeunea aequitexta*	97	*Riccardia smaragdina*
31a	*Prionolejeunea decora*	99	*Brachiolejeunea leiboldiana*
32	*Taxilejeunea pterigonia*	100	*Plagiochila bifaria*
34	*Plagiochila harrisana*	102	*Brachiolejeunea spruceana*
35	*Plagiochila aerea*	103	*Streptopogon calymperes*
38	*Harpalejeunea* sp.	105	*Diplasiolejeunea* sp.
39	*Drepanolejeunea infundibulata*	106	*Frullania apiculata*
39a	*Microlejeunea colombiana*	107	*Frullania sp. 5*
40	*Metzgeria decipiens*	109	*Pallavicinia lyellii*
40a	*Metzgeria leptoneura*	110	*Plagiochila* sp. 7
42	*Frullania brasiliensis*	112	*Rhizogonium novae-hollandiae*
43	*Lepidolejeunea eluta*	113	*Plagiomnium rhynchophorum*
44	*Leiomela bartramioides*	114	*Plagiochila* sp. 8
45	*Ceratolejeunea maritima*	118	*Fissidens serratus*
47	*Plagiochila* sp. 2	120	*Neurolejeunea breutelii*
47a	*Plagiochila* sp. 1	121	*Aneura pinguis*
48	*Ceratolejeunea deciscens*	123	*Leptolejeunea elliptica*
49	*Syrrhopodon graminicola*	125	*Riccardia metzgeriaeformis*
51	*Dendroceros crispus*	127	*Papillaria imponderosa*
52	*Anopolejeunea conferta*	127a	*Meteorium illecebrum*
53	*Lophocolea coadunata*	128	*Zygodon gracillimus*
55	*Trichocholea flaccida*	132	*Plagiochila* sp. 9
56	*Plagiochila* sp. 3	134	*Lejeunea* sp. 3
57	*Prionodon densus*	137	*Frullania* subgen. *Frullania* sp. 1
58	*Trachyxiphium subfalcatum*	139	*Amphilejeunea reflexistipula*
58a	*Trachyxiphium variable*	140	*Colura tenuicornis*

Appendix VI Species List

Epiphytic bryophytes found on three trees, using different methodology, in lower montane cloud forest (2400 m), Yanachaga-Chemillén Range, Peru.

Tree 1, *Alchornea* sp.; Tree 2, *Croton* sp.; Tree 3 *Weinmannia* sp. Both zone 2.1 and 2.2 data from the Weinmannia survey are included here as zone 2.

		Zone					
Family	**Name**	**1**	**2**	**3**	**4**	**5**	**only T**
Mosses							
Bartramiaceae	*Leiomela bartramioides*	*	*	*			
Bryaceae	*Brachymenium consimile*				*		3
Calymperaceae	*Syrrhopodon graminicola* #	*		*			
	Syrrhopodon prolifer var. *cinncinatus*	*					1
Daltoniaceae	*Daltonia longifolia*	*	*	*	*	*	
	Leskeodon andicola			*			1, 2
Dicranaceae	*Campylopus anderssonii*			*	*		1, 2
	Holomitrium arboreum	*		*			1, 3
	Holomitrium sinuosum #			*	*		1, 2
Fissidentaceae	*Fissidens intramarginatus*	*					1
	Fissidens serratus	*					3
Hypnaceae	*Mittenothamnium reptans*	*	*	*	*		
Hypopterigiaceae	*Hypopterigium tamarisci*	*	*				3
Macromitriaceae	*Macromitrium aureum*		*	*	*		
	Macromitrium longifolium				*		3
	Macromitrium podocarpi				*		3
Meteoriaceae	*Meteoridium remotifolium*	*	*	*	*		2, 3
	Meteorium illecebrum			*	*		3
	Papillaria imponderosa		*	*	*		3
	Squamidium leucotrichum				*		3
	Squamidium livens			*			1
Mniaceae	*Plagiomnium rhynchophorum*	*	*				3
Orthotrichaceae	*Zygodon ehrenbergii*		*				3
	Zygodon gracillimus #			*			3
	Zygodon obtusifolius		*				3
	Zygodon reinwardtii	*	*	*	*	*	
Pilotrichacea	*Trachyxiphium glanduliferum* #			*			3
	Trachyxiphium subfalcatum	*					2, 3
	Trachyxiphium variabile	*					2
	Lepidopilum caviusculum #	*	*		*		3
	Lepidopilum scabrisetum	*	*	*	*		
	Cyclodictyon roridum	*					1
Pottiaceae	*Streptopogon calymperes*				*		2, 3
	Trichostomum brachydontium	*	*	*			1, 3
Prionodontaceae	*Prionodon densus*	*	*		*		2, 3
Rhizogoniaceae	*Leptotheca boliviana*			*			1
	Rhizogonium novae-hollandiae	*					3
Sematophyllaceae	*Sematophyllum galipense*	*					3
Thamnobryaceae	*Porotrichum longirostre*	*	*	*	*		
	Porotrichum substriatum	*		*			3
Thuidiaceae	*Thuidium peruvianum*	*	*				

- Not previously recorded in Peru

Family	Name	Zone 1	2	3	4	5	only T
Hepatics							
Acrobolbaceae	*Acrobolbus antillanus*			*	*		1, 3
Adelanthaceae	*Adelanthus decipiens*			*			1
Aneuraceae	*Aneura pinguis*			*	*		3
	Riccardia metzgeriaeformis		*	*	*		3
	Riccardia smaragdina #	*					3
Anthocerotae	*Dendroceros crispus*	*	*	*	*	*	1, 3
Calypogeiaceae	*Mnioloma cyclostipa*	*			*		1, 3
Cephaloziellacea	*Cephaloziella granatensis* #		*				3
Geocalycaceae	*Leptoscyphus physocalyx*				*		3
	Leptoscyphus porphyrius		*	*	*		1, 3
	Lophocolea coadunata	*		*			2, 3
	Lophocolea muricata	*		*			
	Lophocolea sp. 1	*	*	*			
	Lophocolea trapezoidea			*			3
Herbertaceae	*Herbertus divergens*		*	*			1
Jubulaceae	*Frullania apiculata* #			*	*	*	1, 3
	Frullania brasiliensis		*	*	*	*	3
	Frullania riojaneirensis	*	*	*	*	*	
	Frullania sp. 1			*	*	*	3
	Frullania sp. 5					*	
	Frullania stenostipa #					*	3
	Jubula pennsilvanica subsp. *bogotensis* #	*					3
Lejeuneaceae	sp. 2					*	3
Lejeuneaceae (Tribe Brachiolejeuneae)	*Brachiolejeunea leiboldiana* #	*		*	*		2, 3
	Brachiolejeunea spruceana #				*	*	
	Diacranolejeunea axillaris	*	*	*	*		2, 3
	Neurolejeunea breutelii #		*	*	*		3
	Odontolejeunea lunulata		*	*		*	1, 3
Lejeuneaceae (Tribe Cololejeuneae)	*Colura tenuicornis*					*	3
	Diplasiolejeunea sp.				*	*	2, 3
Lejeuneaceae (Tribe Lejeuneae)	*Amphilejeunea reflexistipula* #				*	*	3
	Anopolejeunea conferta	*	*	*	*	*	
	Aureolejeunea fluva #					*	3
	Ceratolejeunea deciscens #	*		*	*	*	
	Ceratolejeunea maritima #	*	*	*	*		1, 3
	Cheilolejeunea comans #		*	*	*	*	
	Cheilolejeunea subgen. *Strepsilejeunea* sp. 1			*	*		1, 2
	Cheilolejeunea subgen. *Strepsilejeunea* sp. 2					*	3
	Drepanolejeunea inchoata var. roraimae			*	*	*	3
	Drepanolejeunea araucariae var. *araucariae*	*	*	*		*	1, 3
	Drepanolejeunea infundibulata #	*	*	*	*	*	
	Drepanolejeunea valiae #					*	3
	Harpalejeunea sp.	*	*	*	*	*	
	Lejeunea sp. 1	*		*			

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Family	Name	Zone 1	2	3	4	5	only T
Lejeuneaceae (Tribe Lejeuneae)	*Lejeunea* sp. 3			*	*		3
	Lejeunea subgen. *Nanolejeunea* sp. 1	*	*	*	*	*	
	Lejeunea subgen. *Lejeunea* sp. 1	*	*	*	*	*	
	Lejeunea subgen. *Lejeunea* sp. 2	*	*	*	*	*	
	Lejeunea subgen. *Lejeunea* sp. 3					*	3
	Lepidolejeunea eluta	*	*	*	*	*	
	Lepidolejeunea spongia #		*	*			2, 3
	Leptolejeunea elliptica		*				3
	Macrolejeunea pallescens	*	*	*	*	*	
	Macrolejeunea pallescens fo. *lancifolia*	*	*	*	*		
	Microlejeunea colombiana				*	*	3
	Omphalanthus filiformis	*	*	*	*	*	
	Oryzolejeunea sp. *(* ad. aff. *O. venezuelana)* #		*	*	*	*	
	Prionolejeunea aequitexta #	*	*				
	Prionolejeunea decora #	*	*				
	Taxilejeunea pterigonia	*	*	*	*		
Lejeuneaceae (Tribe Ptychantheae)	*Frullanoides densifolia* subsp. *densifolia*		*	*	*	*	
Lepidoziaceae	*Arachniopsis diacantha*	*					1
	Bazzania breuteliana	*		*			1
	Lepidozia caespitosa	*		*			1, 3
	Lepidozia sp. 1			*			1
Metzgeriaceae	*Metzgeria decipiens*	*	*	*	*	*	
	Metzgeria filicina		*				1
	Metzgeria leptoneura	*	*				3
	Metzgeria polytricha	*					2
Monocleaceae	*Monoclea gottschei*	*					3
Pallaviciniaceae	*Pallavicinia lyellii*	*		*			3
Plagiochilaceae	*Plagiochila aerea* #	*	*	*			
	Plagiochila bifaria	*	*	*	*	*	
	Plagiochila harrisana #	*		*	*		1, 3
	Plagiochila sp. 1		*	*	*	*	
	Plagiochila sp. 2			*	*		3
	Plagiochila sp. 3		*	*	*		
	Plagiochila sp. 4			*			
	Plagiochila sp. 5			*	*		2, 3
	Plagiochila sp.6		*	*			
	Plagiochila sp. 7	*	*				3
	Plagiochila sp. 8	*					3
	Plagiochila sp. 9		*				3
	Plagiochila stricta	*	*	*	*		
Radulaceae	*Radula montana*	*	*	*	*		
Scapaniaceae	*Scapania portoricensis* var. *portoricensis*			*			1
Trichocoleaceae	*Trichocholea filicaulis* #		*	*	*		1, 3
	Trichocholea flaccida	*					2, 3
	Mosses	24	20	21	18	2	
	Hepatics	43	45	59	47	36	
	Total	67	65	80	65	38	

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